VARIATION AND COVARIATION IN LIFE-HISTORY TRAITS OF SHARKS

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by

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Sciences

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August 9, 1990

St. John's Newfoundland

ISBN 0-315-61849-3

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Abstract

I used the comparative method to examine the interspecific variation of seven life-history traits across Euselachiians, the modern sharks, in relation to adult body size, phylogeny, mode of reproduction, and ecology. Life-history traits included adult female length, length at maturity, birth length, fecundity, gestation, age at maturity, and life span. Body size accounted for a significant amount of explained variation. Phylogenetic history (order, family, and genus) explained only a small amount of variation and covariation of these life-history traits. Genera within families and families within orders tended to show similar levels of variation in most life-history traits, but a larger proportion of the variance occurred at the family level of analysis. Principal component analysis on a reduced number of traits defined an axis ordering sharks from large fecund forms giving birth to many large offspring and small forms with low fecundity and small offspring. The analysis also defined a secondary gradient in which many small offspring versus few large offspring resulted in an inverse relationship between fecundity and birth length. Perception of these patterns of covariation fit r/K selection theory. Analysis within individual families revealed differences from family to family in distribution along the first principal component. Patterns of covariation at the family level appeared also to be constrained by mode of reproduction (oviparity vs viviparity strategies) interacting with size. There is some evidence to indicate that the patterns of covariation may be partitioned according to the mode of reproduction, with a separate axis defining each mode. Ecological associations

appeared to have some effect on the evolution of life-history traits, independent of size and phylogeny. Dietetic and habitat differences were linked to the pattern of covariation of life-history traits. Birth length differences were associated with geographic distribution, and gestation differences were associated with inshore or offshore residency. The comparative method was useful in suggesting the kinds of attributes and ecological relationships that could be used in detailed comparisons of life-histories at the intraspecific level.

Acknowledgments

The author wishes to thank Dr. R. L. Haedrich, Department of Biology, for his supervision and guidance in choosing this topic. Special thanks to Dr. D. Morris, Department of Biology Committee member, for introducing me to the inspiring field of evolutionary ecology and his guidance in the format of this project. Special thanks also go to my other committee member, Dr. J. C. Rice, Department of Fisheries and Oceans, for his many hours of statistical advice and guidance.

The author is indebted to the Department of Fisheries and Oceans, Canada, for financial contributions.

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Introduction

The concept of life-history tactics (patterns) describes a complex co-adaptation of traits resulting from natural selection in a specific environment involving trade-offs among reproduction and survival of a species (Stearns 1976, 1977). The relationship of these trade-offs and aspects of the environment are poorly known but usually have been described according to r and k selection theory (MacArthur and Wilson, 1967; Southwood et. al., 1974; Southwood, 1976) and/or optimal life-history theory (Gadgil and Bossert, 1970). Various early studies of life-history traits within groups of related organisms pointed to a strong tendency for these traits to co-vary along a single axis which was often called the r-K continuum after Pianka (1970). This axis places short-lived species at one end - which mature early, with large reproductive efforts, and many small young - to long-lived and late-maturing species with smaller reproductive efforts and a few large young. Under r and k selection theory, the best life-history strategy would be a compromise between the conflicting demands of reproduction and survival. This point of compromise for a species would be a result of selection factors operating and this would determine the species position on the r-K continuum (Gadgil and Bossert, 1970; Pianka, 1974). The conclusion from these earlier studies was that not only did the r-K continuum exist but it was the major way in which life-history traits of organisms varied (Stearns, 1977). The appeal of this concept is that one can predict that a certain group of traits would usually be found in r-selected species or in K-selected species. There is a tendency to think that r-selected species or K-selected species are end

points of a continuum. However, species will have many different selective forces acting on them in both spatial and temporal ways; and this will dictate their position along the continuum (Adams, 1980). General theories from these early studies have been proposed to predict the response of life-history traits to natural selection by ecological factors. As Horn and Rubenstein (1984) stated, "natural selection favours those individuals who most abundantly transmit copies of their genes to future generations. This task demands appropriate allocation of limited resources between conflicting requirements of reproduction and survival in an environment which is at best capricious and at worst predictably hostile." The resultant life-history is described by a schedule of fecundity and survival in which age-specific, environmental-specific, and individual-specific factors can bring about changes related to the demands of allocation of limited resources through natural selection.

Recent studies have criticized r/K selection, showing several incidents that predict different results and noting that K, the population carrying capacity, is not subject to selection (Wilbur et. al., 1974; Stearns, 1977, 1980). Stearns (1977) analyzed 35 studies of selection regimes and found that half of them did not fit r/K selection theory. These studies have found that the patterns of covariation existed but cannot be explained by density dependent or density independent mechanisms of population regulation. Perception of the patterns of covariation, thought to be described by r/K selection theory, became the focus of research in the 1980s. If life-history tactics are studied at the intraspecific level, patterns of covariation

in life-history traits often elude demonstration (Stearns, 1980; Dunham, 1982). Stearns (1980) also pointed out that life-history tactics at the intraspecific level may be constrained by allometric relationships and that life-history traits show strong interactions with physiology, genetics, development, or behaviour. Because of this, Stearns (1980, 1983, 1984) predicted that when comparisons are made across many taxa or at higher taxonomic levels, patterns of covariation - i.e., coadaption - would be more obvious and stronger. Stearns argues that the complex interactions of physiology, genetics, and development at higher levels of taxonomy become less important than at the intraspecific level. These interactions, coupled with the fact that if it can be demonstrated that allometric constraints are stronger within lineages than among lineages, tactics would be clearer in interspecific comparisons at higher levels of taxonomy. Stearns's (1984) paper on life history variation in reptiles received severe criticisms involving errors in his data (Vitt and Seigel 1985), errors in statistical procedure (Dunham and Miles 1985) error in choice of length in oppose to weight as measure of body size (Hedges 1985), and lack of attention to environmental and ecological variables (Dunham and Miles 1985; Hedges 1985). However, when Dunham and Miles (1985) repeated the analyses with corrections to the data and statistics similar results were achieved.

Since Stearns's 1977 review of selection regimes, several other studies have emphasized that life-history variation is more discernible when comparisons are made across many species or when they are made at higher taxonomic levels. Covariation of life-history traits at the

family level or higher were detected in Stearns's studies of mammals (1983) and reptiles (1984), Brown's (1983) work on freshwater snails, Dunham and Miles's (1985) work on reptiles, Hutchings and Morris's (1985) work on salmonids, Gittleman's (1986) work on carnivores, and Harvey and Clutton-Brock's (1985) work on primates (using subfamilies). Covariation of life-history traits in these studies were analyzed by controlling the effects of allometry and phylogeny. Dunham and Miles (1985), Gittleman (1986), and Harvey and Clutton-Brock (1985) also considered the relationship of ecology and life-history variation as did Murphy (1989) in his work on North American tyrant flycatchers.

Stearns (1983, 1984) showed that the strength of patterns of covariation in life-history traits in any comparison is influenced by body size, independent of phylogeny. Most life-history traits are known to be scaled to body size, and it may be considered the most important covariate of life-history traits (Blueweiss et al., 1978; Western and Ssemakula, 1982; Peters, 1983; Calder, 1984). Mammalian life-history tactics were found to be constrained by body size and phylogenetic covariation (Stearns, 1983; Gittleman, 1986). Stearns (1983) defined a primary tactic of r/K strategists and a secondary tactic of altricial to precocial forms in mammals. Size and phylogenetic covariation in life-history traits among reptiles also defined a primary tactic of r/K strategists (Stearns, 1984). Dunham and Miles (1985) showed that this phylogenetic gradient in reptiles could be further partitioned by mode of reproduction. Within the family Salmonidae, Hutchings and Morris (1985) found that size alone did not appear to affect patterns of covariation in life-history traits

of salmonid fishes but that lifestyle (i.e., anadromous migrant vs freshwater residency) of anadromy had greater influence on covariation of life-history traits. Harvey and Clutton-Brock (1985) found a significant amount of variation in life-history of primates was explained at the subfamily level and that this variation was highly correlated with variation in body size. These differences in body size were associated with differences in behaviour and ecology. Murphy (1989) concluded that phylogeny had little impact on variability in reproductive traits and that most interspecific differences were attributed to ecological influences in North American breeding tyrant flycatchers. These studies attempted to identify the circumstances in which life-history tactics are adaptive by comparing groups of species living in different circumstances (Bell, 1989).

Phylogeny is usually a poorly-defined variable that refers to variability associated witn unique features of an evolutionary line, often at the level of order or family (Murphy, 1989). Taxonomy is assumed to represent phylogeny. Hence, taxonomic levels are used to reflect levels of relatedness - i.e., ancestry. However, any ecological differences that may exist among groups of species must be included (Hedges, 1985; Gittleman, 1986; Murphy, 1989). Dunham and Miles (1985) concluded that the way a species reproduces should also be considered as a likely determinant of life-history variation. They concluded that the axis of life-history variation in reptiles could be partitioned according to the mode of reproduction and brood frequency.

As a result of these research efforts, body size appears as a central covariate in life-history patterns more or less being closely linked to traits that describe a species fitness. To understand life-history variation, we need to know all important covariates of life-history traits. These covariates must be analyzed and their complex tangle of interactions must be unravelled before most theories of life-history evolution can be tested properly. The extent of the influence of allometry and phylogeny in other groups of organisms and the identification of other covariates are problems that require immediate attention (Hedges, 1985).

Life-history patterns, therefore, differ among species as a result of several simultaneously acting influences. In studying these influences - i.e., allometry, phylogeny, and ecology - on life-history variation, the comparative method was used in all of the above-referenced studies. The comparative method is distinguished from experimental or observation methods by its use of information obtained from comparisons across taxa to test ideas about evolution. The adaptive significance of taxonomic variation in a life-history trait is inferred from the way the character covaries with other characters or with components of the environment (Pagel and Harvey, 1988). This can be achieved by broad base comparisons of related species. As well, Bell (1989) noted that when the comparative method was used to study similarities of related species sharing a common way of existence, one could examine common ancestry and the common cause of modifications in evolution.

In this study, I will use the comparative method to separate the effects of size, phylogeny, mode of reproduction, and ecological correlates on interspecific differences in life-histories of sharks of the subclass Elasmobranchii. Examination of the life-histories of sharks should provide insight as to whether they are constrained by size or phylogeny and ranked along the r-K gradient or are shaped by other microevolutionary forces such as ecology and other factors yet undefined.

Sharks emerged in the late Devonian period around 400 million years ago and are considered one of the oldest living groups of jawed vertebrates (Schaeffer, 1967). Except for some periods of speciation and adaptive radiation, with one branch leading to skates and rays, the sharks have remained remarkably stable (Springer, 1967). They have been abundant throughout the ages despite environmental changes and increased abundance and diversity of competitors. It is thought that the radiation of modern elasmobranchs, sharks and rays, was partly triggered by the evolution of teleosts and these modern species took over the niches of their ancestors as well as invaded new adaptive zones. The stability of these adaptive zones led to the longevity of some families (Thies and Reif, 1985). Sharks live in all parts of the oceans, from shallow to deep waters, and are distributed through all temperature clines, from the tropics to polar regions. They have invaded freshwater to some extent. Sharks have developed a life-history pattern that has not changed much from their beginning (Hoenig and Gruber, 1989). The typical pattern used to describe sharks is long lived, slow growth, late age at maturity, large adult size, and few

well-developed offspring. Unlike teleost fishes, which are generally characterized by rapid growth, early maturity, small size, short life span, and many fragile offspring, sharks have evolved a life-history strategy similar to marine reptiles and mammals (Hoenig and Gruber, 1989). Shark phylogenetic systematics are based on studies of skeletal and morphological features (Compagno, 1973, 1977).

Despite their long history, sharks are not well known. Wourms (1977) published a review on reproduction and development in chondrichthyan fishes, which brought together most of the information known on biology and ecology of sharks. In sharks, all fertilization is internal and most sharks are viviparous - i.e., live-bearers - with a few being oviparous - i.e., egg layers. Wourms (1977) considered that phylogenetic position, geographical distribution, benthic vs pelagic habitat, adult size, feeding ecology, egg-embryo size, and embryonic osmoregulation were factors in the retention of oviparity or the evolution of viviparity in sharks.

Objectives

Measurements of life-history traits in sharks are far from complete. Therefore, I had to subdivide the database frequently to address specific objectives. I divided the study into two main sections: one dealing with covariation among life-history traits; the other dealing with life-history variation and ecology.

Specifically, in section A, I will attempt to answer five questions about the relationship of size, phylogeny, and mode of reproduction to covariation and evolution of shark life-histories: (1) What is the impact of size and phylogeny on life-history variability? (2) How do life-history traits covary in sharks? (3) Do life-history patterns remain after the effect of size and phylogeny are accounted for and if so, are these covariations similar to an r-K continuum? (4) What is the relationship between life-history and mode of reproduction (i.e., oviparity vs viviparity strategies)? (5) What is the relationship between ecological factors and the patterns of covariation? In section B, I will attempt to answer the question: Does occupation of various ecological conditions help shape life-history variation in sharks?

Materials

Data source:

I compiled a list of 344 species in 8 orders, 30 families, and 97 genera from Campagno's (1984) two-volume catalogue entitled, "Sharks of the World." The classification system used was based on Campagno's (1973) phyletic nomenclature (Fig. 1). Information on life-history and ecological variables were taken from these two volumes and supplemented with additional data published since 1984 (see Appendix 1). Data on sharks are somewhat limited because sharks are not well studied. Most information comes from commercial fisheries or museum specimens.

From this 344-species list, only 247 species, belonging to 8 orders: 20 families; 79 genera, were extracted to be used here. Information was not used on the following families: Chlamydoselachidae, Brachaeluridae, Cetorhinidae, Pseudotriakidae, Leptochariidae, Stegostomatidae, Rhiniodontidae, Mitsukurinidae, Pseudocarchariidae, and Megachasmidae. Not all variables were available for each species (see Appendix 1). The incomplete data meant that although broad patterns could be sought among 247 species, detailed consideration of the relationship of some life-history traits to others was hampered. Exact sample sizes are presented for each analysis (see Appendix 2).

Quality of data:

In any broad survey, the quality of the data is inevitably variable. Only observations made on sharks collected in the wild were used; species records from museums were not included. Because this analysis will focus on interspecific comparisons, not intraspecific, the inclusion of several measurements of the same trait for the same species can inflate sample size and produce results that may be misleading. Therefore, when measurements of traits for some species were cited as a range, the mid-point of that range was selected to represent the value of that trait. Although any attribute that affects fitness can be considered in studying life-histories of sharks, the analyses were restricted to those that were generally reported in the literature.

The attributes:

The life-history traits, each representing a trade-off in costs and benefits, used in the analyses in section A and section B were:

1. Length (female) (cm): maximum body size recorded. This attribute is the most common because it is the easiest size trait to measure. Data on body weights or any other size variable are seriously lacking. Sexual dimorphism in sizes of sharks is nearly universal with females usually attaining larger sizes than males.

2. Length at maturity (female) (cm): This attribute in fishes is generally one that shows response to density dependent mechanisms. Here, it is the size reached at first maturity.

3. Birth length (cm): All sharks are born or hatched in a well-developed form and this size is used here.

4. Fecundity: Refers to the number of offspring born per litter. Egg counts were not used because not all become fertilized and some may be cannibalized in the uterus.

5. Gestation period (months): All fertilization of eggs in sharks is internal. Time recorded from conception to birth was used to measure gestation length whether the embryos were developed internally (viviparity) or externally (oviparity).

6. Age at maturity (female) (years): This attribute describes the age at which first maturity is reached.

7. Life span (female) (years): Sharks are among the longest lived fishes; but due to difficulty in obtaining age samples (usually vertebra) and difficulties in ageing, oldest ages are not known for many species. Long life span is usually associated with large body size (Blueweiss et al., 1978).

8. Mode of reproduction: All sharks are iteroparous and there are two general types of reproduction in sharks. The first type is oviparity in which fertilized eggs are deposited on the bottom of the ocean and the young hatch into a well-formed state. The second type, which shows tremendous variation, is viviparity in which fertilized eggs develop inside the female and are live-born. Developing embryos in viviparous species have nutrients fed either by aplacental (egg reserves) or placental attachments to the female and in some oviphagous (uterine cannibalism) embryos occur. All sharks produce young annually, biannually, or every other year; however, brood frequency data on most sharks are not available.

The ecological variables. Each species was assigned to one type in each of the following ecological categories deemed important from Wourm's (1977) work:

1. Diet - primarily feeders of (a) plankton[1], (b) benthic invertebrates and some small fish, (c) mostly small and large fish, and (d) omnivorous - not feeding predominately on any one type of food.

2. Habitat Types - strictly benthic or bottom dwellers, strictly pelagic or off-bottom dwellers, and pelagic/benthic dwellers.

3. Zonation - strictly inshore or coastal dwellers, strictly offshore or deepwater shelf dwellers, and oceanic or inshore/offshore dwellers.

4. Region - distribution of species inhabiting northern oceans above the equator, southern oceans below the equator, and cosmopolitan inhabiting both northern and southern oceans.

SECTION A

Methods

The level of significance used in all statistical tests was 0.05. All statistical computations were done using routines in SAS (SAS Institute Inc. 1985).

1. Plankton feeding sharks were eventually not used in the analysis due to lack of data on their life-history traits.

1. Univariate statistics and impact of size (228 species)

I log-transformed female body length, length at maturity, birth length, fecundity, gestation, age at maturity, and life span. Log transformation was done to stabilize variance by making variances independent of the mean. Its success was determined by examination of values calculated for skewness and kurtosis. Mode of reproduction was not included due to problems of using binary variables in regression analysis because they do not conform to the assumptions in these models (Gower, 1966; Dunham and Miles, 1985). Least square regression was used to remove effects of size by regressing the 6 life-history traits against length (size). Model I regression - i.e., least-squares - was chosen because it is the only line-fitting method that gives deviation scores or residuals which can be used in other analyses of interest. These residuals represent variation in a trait away from the expected trend and are used as independent points. The residuals were retained for analyses among taxa. I then calculated Pearson product-moment correlation coefficients to determine closeness of linear relationships of all life-history traits with each other. I also calculated Pearson product-moment correlation coefficients on the residuals from the regression analysis of each life-history trait on size.

2. Phylogenetic effects (4 orders, 16 families, 228 species)

Nested analysis of variance (ANOVA), using unequal sample sizes, on the log-transformed data was used to partition the total variation of each life-history trait into components due to membership of species in the taxonomic levels of order, family, and genus. As well, the percentage of variance in each life-history trait associated with each level was estimated. Partitioning of the total variation using nested ANOVA dealt with the levels of order and family comprising the classification variables. Concern as to whether or not any comparative trends seen at the order and family levels were not taxonomic artifacts, the analysis using nested ANOVA was also extended to a lower taxonomic level to see if the same trends existed in variation partitioning. There were not enough genera with more than two species to make a three-level analysis possible. Two such analyses of variance (ANOVA) were calculated: one with the effects of size retained, and one with size effects removed by using the residuals from the regression analysis. By examining whether the amount of variation in life-history traits at various taxonomy levels was small or large allows the nested ANOVA to point to the level that further analysis should concentrate - i.e., the level with the most variation (Pagel and Harvey, 1988). Only orders with 2 or more families and families with 2 or more species were used, following Stearns's (1983, 1984) protocol.

3. Mode of reproduction

Mode of reproduction is a two-state variable in sharks; 58 of the species used in this analysis are oviparous and 189 species are viviparous. I re-analyzed the effects of size and phylogeny on all life-history traits according to whether species were oviparous or viviparous. Two one-way ANOVAs, with unequal sample sizes, were used to partition the total variation of each life-history trait into components due to family level taxonomy (phylogeny) according to how the species reproduce. A two-level nested ANOVA was not possible because the oviparous mode of reproduction was not well distributed across either orders or genera. Mode of reproduction is not a familial characteristic in sharks.

4. Covariation among life-history traits

I obtained complete life-history data for only 18 species. Consequently, because sample sizes were low for traits such as gestation period, age at maturity, and life span, I excluded them from the initial analysis of covariation of life-history traits leaving 81 species (10 families) (Appendix II). I analyzed length, length at maturity, birth length, and fecundity using these 81 species to test for patterns of covariation. I selected only families with two or more species; consequently, order level analysis would be restricted to only one order and was not used.

Principal component analysis was used to determine patterns of covariation in the reduced set of life-history traits. I performed two principal component analyses on all 81 species. One was on the original data which included effects of size. The other was on residual values after the effects of size were removed by regression of each life-history trait on length (i.e., length was the covariate in the linear model).

In the principal component analysis (PCA), I used correlation matrices, instead of covariance matrices, because measurements of life-history traits were in different scales - i.e., centimeters, counts, months. Pimental (1979) noted that if scales of measurement differ, their variance and covariance are not comparable, and the PCA should be performed on a correlation matrix. Phylogenetic effects of family and genus were removed in a four-step analysis, with and without the effects of size included, to study the effect of phylogeny on covariation of life-history traits using general linear models. This was done by fitting a series of linear models, with an increasing number of terms, to the original data from the 81 species in the 10 families. In each case, the residuals from the linear model were analyzed with PCAs to examine patterns in covariation after the effects of the terms in the model were removed. The first model included only a term for family level effects as a categorical variable with 10 levels. The second model included both the length effects as a forced covariate (i.e., it entered the model before other terms) and the categorical variable for family. The

third model included terms for both family and genus, as another categorical variable (14 levels) nested within family. The fourth model contained the forced length covariate and the two categorical variables - family and genus nested within family. The genus level analyses were restricted to genera containing two or more species, leaving a sample of 63 species in 9 families and 14 genera. In this way, I was able to look at the impact of size and phylogeny on patterns of covariation in life-history traits.

Within five families: Squalidae, Triakidae, Carcharhinidae, Sphyriniidae, and Scyliorhinidae, there were enough species (5 or more) to examine whether patterns of covariation within families were the same as patterns found across families. Size effects were removed through regression of each trait on length and the residuals were run in a principal component analysis for each family separately. Within one family: Carcharhinidae (3 genera, 24 species), I examined the effects of genus after removal of family and size effects using a general linear model with the length effects as the forced covariate and the categorical variable for family (one level). These across and within taxa comparisons are a means of estimating whether covariation in life-history traits contain a phylogenetic component.

The purpose of using principal component analysis was to see if there is a non-random pattern to the variation in the data sets. By doing successive model fittings and PCAs, one can see if significant variance is associated with size and phylogeny. As

well, one can see if having removed the effects of the model terms whether the patterns of residual variation were altered by comparing the PCA structure and corresponding correlation structure of successive PCAs of residuals.

Results

1.0 Univariate patterns

Summary of mean values for each family indicated considerable variation across families (Table 1). Among families, average length ranged from 50.0 to 470.3 cm, average length at maturity ranged from 26.9 to 325.2 cm, average birth length ranged from 12.3 to 105.2 cm, average fecundity ranged from 2.0 to 21.2, average gestation period ranged from 7.5 to 20.3 months, average age at maturity ranged from 3.9 to 6.3 years, and an average life span ranged from 15.5 to 28.9 years. Mode of reproduction values were coded 0 (for oviparous), 1 (for viviparous), and three families were coded for a mixture of both types of mode of reproduction (0+1).

1.1 Impact of size

Examination of values of kurtosis and skewness indicated that the log-transformation of the values of life-history traits was relatively successful in stabilizing the variance (Table 2). Regression analysis on log-transformed values of length at

maturity, birth length, fecundity, age at maturity, and life span revealed significant relationships with size in five out of six life-history traits (mode of reproduction not used here) ($P < .05$) (Figs. 2-7; Table 3). Size did not account for any significant variation in gestation period ($P > .05$).

1.2 Correlations among traits

Pearson product-moment correlation analysis of all traits with the effects of size included (Table 4) and removed (Table 5) showed the influence size can have on correlation among traits.

(a) Length at maturity. Before removal of size, length at maturity was significantly correlated with birth length, fecundity, age at maturity, and life span ($P < .05$) but not gestation period ($P > .05$). After removal of size, only the correlations with birth
length and age at maturity remained significant ($P < .05$) but their levels of association were lower.

(b) Birth length. With size effects included, birth length was significantly correlated with length at maturity, age at maturity, and life span. Upon removal of size, all correlations lost their significance ($P > .05$) but it resulted in a significant negative correlation with fecundity ($P < .05$). Least-squares regression analysis was used to see how the effect of size was masking this underlying negative

correlation. Regression of fecundity against birth length (with size effects included) indicated a positive but weak correlation ($r = .17$, $P = .08$) (Fig. 8). Removal of the effects of size resulted in a negative correlation indicating that size confounded the relationship. An expected increase in size at birth would result in a lowering of fecundity to accommodate this in sharks (Fig. 9).

(c) Fecundity. Before removal of size, fecundity was only significantly correlated with length at maturity ($P < .05$); however, this correlation disappeared with the removal of size, resulting in a significant negative correlation only with birth length ($P < .05$).

(d) Gestation period. There was no significant correlation between gestation period and any other life-history traits when size effects were included or removed ($P > .05$).

(e) Age at maturity. This trait was significantly correlated with length at maturity, birth length, and life span ($P < .05$). Upon removal of size effects, only significant but lower correlations with length at maturity and life span remained ($P < .05$).

(f) Life span. This trait was significantly correlated with length at maturity, birth length, and age at maturity ($P < .05$) before removal of size effects. After removal of effects of size, only the significant correlation with age at maturity remained ($P < .05$).

1.3 Summary

Examination of the correlation matrices showed many significant pair-wise correlations among all traits, except gestation period, when the effects of size were included. Removal of size effects, in most cases, reduced the level of associations. However, one new significant correlation emerged with removal of size effects: a negative correlation between fecundity and birth length. The true relationship of these latter two traits was probably masked by the influence of size.

2.0 Phylogenetic effects

2.1 Order and family levels

Partitioning the variance in life-history traits using a two-level nested ANOVA, with size included, revealed significant variation in length, length at maturity, birth length, fecundity, and gestation period at both the order and family levels ($P < .05$). No significant variation was detected in the analyses of age at maturity and life span ($P > .05$) (Table 6). Significant

variation in individual life-history traits in sharks was stronger at the family level when variance components were compared to the order level.

With the removal of size effects, significant variation in birth length, fecundity, and gestation period remained in both the order and family levels. Significant variation in age at maturity was found only at the order level while significant variation in length at maturity was only found at the family level ($P < .05$). At the family level removal of size caused greater reduction in the average variance explained (28% to 16%) while little change was evident at the ordinal level (Table 6).

Order effects on length at maturity and age at maturity appeared to be size mediated. Significant family effects detected in any life-history trait were not lost after the removal of size although the effect of size removed was more obvious than at the order level. Size alone does explain a large amount of variation seen at higher taxonomic levels. Because residual variation was high in the nested ANOVA involving order and family levels, I decided that it was appropriate to see if the cause of some of this high residual variation might be due to variation at a lower taxonomic level - i.e., genus. I selected only those families with two or more genera and genera with two or more species for a

total of 6 families, 28 genera, and 159 species. I repeated the two-level nested ANOVA with the classification variables being family and genus nested within family.

2.2 Family and genus level

Partitioning the variance in life-history traits using the two-level nested ANOVA, with size effects included, showed similar results found in the order and family level analyses. Significant variation in length, length at maturity, birth length, and fecundity were found at both the family and genus levels ($P < .05$) (Table 7). As well, significant variation in gestation was only found at the family level. No significant variation was found in age at maturity and life span at both levels ($P > .05$). Again, significant variation in individual life-history traits in sharks was strongest at the family level.

Removal of size effects greatly diminished the average proportion of family-level variance (47% to 35%) due to decrease in variation in length at maturity, birth length, and fecundity (Table 7). The average proportion of life-history variance at the genus level slightly increased from 19% to 20%. Significant differences in the amount of variance explained at the family level was found in all traits except age at maturity and life span. Upon removal of size effects, the amount of variance explained by age at maturity became highly significant. Family effects were only detected for age at maturity, indicating that

this trait may be size dependent. Significant genus effects were found in length at maturity, birth length and fecundity and remained after removal of size effects (Table 7). Average proportion of life-history variance accounted for by residuals increased (34% to 45%) but was lower than the amount calculated for order-family analysis.

2.3 Summary of results

Among order levels in sharks, significant variation was found in length, length at maturity, birth length, fecundity, and gestation period. When size effects were removed, significant differences in length at maturity were lost while significant differences now became noticeable in age at maturity. Among families, significant variation was also found in the same traits as at the order level and removal of size effects did not change these differences. Among family and genus levels, significant variation was also detected in length, length at maturity, birth length, and fecundity (family only). Removal of size effects resulted in significant variation being seen in age at maturity while no change was observed in the other life-history traits at both the family and genus levels indicative of little impact of size.

Both sets of results suggest that most variability in life-history traits of sharks can be accounted for by differences among families. Genera within families did not add substantial variance

that was independent of phylogeny; i.e., any genus could be a relatively good predictor for other genera in its family. However, such is not the case for families within orders where the average value of a life-history trait in one family would not, in most cases, be a good predictor of the average value in other families.

After size effects were removed, significant differences were found for some life-history traits at the order, family, and genus levels representing phylogenetic history. Since it is strongest in families, further analyses should concentrate at this level. Some orders are represented by very few families which would bias interpretation of further analyses because of species-rich orders.

3.0 Covariation of life-history traits

The results of a six-step principal component analysis to determine impact of size and phylogeny (family and genus) on patterns of covariation in life-history traits in sharks are presented in Tables 8 and 9. Correlation analysis among traits is shown in Table 10.

3.1 Analyses among families and genera

With size in the model, the first principal component (PC1) explained 76% of the variance in the data; and upon removal of size effects, only 55% of the variance was explained (Table 8A).

The corresponding reduction in variance (0.5% to 5%) explained by PC1 upon removal of family and genus effects was very small in comparison (Table 8B). The second principal component (PC2) showed a corresponding increase in the amount of variance explained by the removal of size effects (Table 8B).

Interpretation of the component loadings on PC1 revealed a pattern of covariation that explained most of the variability in the data. It remained throughout and described an axis consisting, at one end, of small sharks, maturing at a small size, having low fecundities, and small size at birth to large sharks with the opposite suite of traits at the other end (Table 9A). Component loadings on PC2 described a second axis relating fecundity with birth size ranking sharks, at one end, with low fecundity and large size at birth to sharks with high fecundity and small size at birth (Table 9B). These two axis describe covariation in life-history traits as would be expected from r/K selection theory. The first axis described a size component found in all three taxonomic levels.

Removal of size, family, and genus effects changed the size component axis in PC1 (Table 9A). Removal of size effects removed the correlations between the life-history traits that existed at all taxonomic levels and unmasked an underlying negative correlation between fecundity and birth length (Tables 10D,E,F). The axis now represented small maturing sharks with many small offspring versus large maturing sharks with few large offspring.

After removal of size effects and subsequent removal of phylogenetic effects, the original pattern was lost. The second pattern perceived as a fecundity/birth size seen in PC2 disappeared upon removal of size and phylogenetic effects (Table 9B). Component loading on PC3 showed no discernible patterns and accounted for the least variation (Table 9C).

Plots of PC2 axis scores against PC1 axis scores from the analyses, with size effects included in the model, generally showed that scores were normally distributed on both axes with two-thirds of the scores falling between ± 1.0 standard deviations (Fig. 10). This meant that the pattern of variation represented by PC1 as a size component is a pattern applicable to the full suite of species even with the removal of family and genus effects. Similarily, the pattern of variation seen in PC2 as many small offspring versus few large offspring component seems to be general across all species (Fig. 10-12). Perception of these original patterns seen on both axis were seriously weakened when the effects of size and phylogeny were removed and the plots re-examined. PC1 now described a size-fecundity component axis with small maturing sharks with many small offspring to large maturing sharks with few large offspring (Fig. 13-15). Examination of changes in the correlation matrices showed that with size effects in the model there was no fecundity-birth length relationship but there was a size relationship with all other traits (Tables 9A,B,C). However, when size effects were removed, a fecundity-birth length relationship was found - i.e., many small

offspring versus few large offspring (Tables 9D,E,F). Because the magnitude of the component loadings (eigenvectors) is dependent on off-diagonal correlations, the changes in association between fecundity and birth length to one of contrast seems to be associated with the effect of size. Since the distribution of scores on the response coordinate axes appeared to be normally distributed (i.e. between ± 1 standard deviations), in most cases, additional rotation techniques would not be necessary to find a pattern of loading's more easily interpreted or identifiable with the nature of the present response variables seen in the rigid rotation of the plots.

3.2 Impact of other life-history traits

Inclusion of information in gestation period, age at maturity, and life span into the PCA would have reduced the number of species to 18 and would have made any interpretation of covariation unreliable. Therefore, to determine the possible impact of gestation period, age at maturity, and life span on covariation patterns seen above, if the database had been larger, I generated a correlation matrix using the scores from the first and second principal components from the covariation analyses (Table 11). With size effects included, there was no correlation with the first principal component, although correlations were significant for age at maturity ($r = .61$) and life span ($r = .42$) with the second principal component (Table 11A). With the removal of family effects in a manner similar to that described in the

principal component analyses in the previous section, age at maturity ($r = .53$) and life span ($r = .44$) correlated only with the first principal component (Table 11B). Upon removal of genus effects, no correlations were found (Table 11C).

I concluded that if more data were available on age at maturity and life span, these two traits could be incorporated in discernible patterns of covariation; but gestation period would probably not be included. Based on these correlations, where similar patterns of covariation existed, it would be most obvious at the family level than at the genus or species level.

3.3 Analysis within families

Principal component analysis, with the effects of size removed, were performed separately on five families, each with four or more species, to determine if patterns of covariation seen across families existed within families. The five families were Squalidae, Triakidae, Carcharhinidae, Sphyrnidae, and Scyliorhinidae. PC1 explained an average of 61% of the variance, ranging from 75% in Squalidae to 48% in Triakidae (Table 12). Positive component loadings for length at maturity from PC1 were found in each family (Table 13). Strong loadings for birth length were found for all families except Triakids. The loadings were positive for Squalids, Carcharhinids, and Scyliorhinids but negative for Sphyrnids (Table 13). Positive component loadings for fecundity were found for Triakids and Sphyrnids, while

negative loadings were found for Squalids and Carcharhinids. For Scyliorhinids, the loadings were weak for fecundity. Interpretation of the component loadings on birth length and fecundity for Squalids, Carcharhinids, and Sphyrnids pointed to a fecundity component ranking small maturing sharks that produced many small young to late maturing sharks producing few large young (Table 12). Only Squalidae and Carcharhinidae showed the exact same pattern seen in across family analyses.

Examination of the correlation matrices help explained variations in component loadings within families (Table 14). Birth length was negatively correlated with fecundity in Squalids, Carcharhinids, and Sphyrnids; but correlations were extremely low for Triakids and Scyliorhinids. The lack of correlation in Scyliorhinids can be explained by the fact that all species of this family used in the analysis were oviparous with a fixed fecundity of two. Within the family Triakids, this fecundity-birth length relationship does seem to exist. These independent correlations within families are responsible for variation in component loadings on principal components and within the principal component results. These results indicated that patterns of covariation of life-history traits discernible across several families, were also discernible within families at comparable magnitudes, although variable in sign.

3.4 Analysis of effects of genus

The family Carcharhinidae contained 3 genera with 24 species. An attempt was made to analyze the effects of genus on life-history traits after removal of correlation with size and family (Table 15). No significant variation was found in length at maturity, birth length, or fecundity at this level ($P < .05$). Within Carcharhinidae, there appeared little variation among genera and no effects of genus on the three life-history traits were detected.

3.5 Summary of results

How do life-history traits covary in sharks? Principal component analysis defined a size component axis ordering sharks from small, maturing at a small size, having low fecundity, and giving birth to small young to large sharks with the opposite suite of traits. A second axis was also defined describing a trade-off in fecundity: many small offspring vs. few large offspring. These are typical patterns expected under r/K selection theory.

How are the patterns of covariation influenced by size and phylogeny? Size alone explained the pattern of covariation in life-history traits. Removal of the family and genus effects had little effect on the patterns of covariation. However, after the removal of the effects of size, family, and genus effects, the

original pattern of covariation perceived as r-K selection on PC1 axis was weakened. Species were now ordered on an axis consisting of small maturing sharks with many small offspring to large maturing sharks with few large offspring. Thus, removal of phylogenetic effects has an overall effect on patterns of covariation. This was seen in the changes in polarity in the factor loadings on fecundity and changes in structure of the correlation matrix. Removal of size and phylogenetic effects in the PC2, describing the fecundity/birth size, caused this relationship to vanish and the PC2 then showed a body size-fecundity relationship.

In the within family analysis, the amount of variation explained by the first principal component varied from lineage to lineage as did loadings of each trait on that component. Pairwise correlations of traits also differed in comparable ways across families. After removing size and family effects within Carcharhinidae, there were no significant residual genus effects, although with only 3 genera, the test may not have been as strong as tests of other factors. Patterns of variation in length at maturity, birth length, and fecundity suggest lineage dependency. Across and within family level differences represent the influence of phylogeny on covariation of life-history traits in sharks.

4.0 Mode of reproduction effects

The nested ANOVA method provided an estimate or a focal point on where to concentrate the analysis. Thus far, mode of reproduction has not been considered due to statistical problems with binary data previously mentioned. Therefore, I re-analyzed the effects of size and family on all life-history traits according to how sharks reproduced - i.e., oviparity vs. viviparity - using two one-way ANOVAs with family as a classification variable.

Oviparous species showed significant family variation only in length and fecundity ($P < .05$). After removal of size, significant family variation in fecundity remained ($P < .05$) (Table 16). Viviparous species showed significant family variation for length, length at maturity, length at birth, fecundity, and gestation ($P < .05$). After removal of size, all significant family variation remained; and significant variation was also found in age at maturity ($P < .05$) (Table 16). The explanatory power (R^2) of the models increased from the oviparous to viviparous mode of reproduction.

These results suggest that the PCA structure be examined according to mode of reproduction. Four separate PCAs were run on the 81 species using the same life-history traits, with phylogenetic (family) effects removed according to whether the species were oviparious (9 species in 2 families) or viviparous

(72 species in 8 families) with and without the effects of size included in the models. A similar amount of variance was explained by PC1 and PC2 in all PCAs (Table 17). However, only the component structure for viviparous species matched the overall PCA (from the family level analysis) described with size effects in the model (Table 18). In oviparous species, fecundity is small or fixed at 2 offspring; hence, the underlying fecundity-birth length component does not exist as verified by the correlation matrices (Table 19). Although the sample size is small for oviparous species in the PCA, combined results of the ANOVAs and the PCAs suggest that the phylogenetic gradient could be divided according to how sharks reproduce - i.e., they do not share the same common axis.

4.1 Ecological factor effects

The effects of ecological variables such as diet, habitat, zone, and region on patterns of covariation of life-history traits, after factoring out phylogenetic (family) effects, were examined using two factorial ANOVAs, one with size effects in the model and one with size effects removed. Scores from the principal component analysis on 81 species, with family effects removed, were entered as dependent variables. With size effects in the model, only diet showed any significant relationship with the size gradient of PC1 ($P < .05$), diet was marginally significant ($P = .0679$) (Table 20). After removal of size effects, no significant relationships were found between any

ecological variables and PC1 scores; however, habitat showed a significant relationship with the PC2 scores ($P < .05$) (Table 20). This suggests that the pattern of covariation in length, length at maturity, birth length, and fecundity may be influenced by some specific ecological factors even after phylogenetic effects had been removed.

SECTION B

Life-History Variation

Methods

In this analysis, individual life-history traits were analyzed separately to explore the effects of size, phylogeny, mode of reproduction, and ecology on life-history variation. Life-history traits not used in the covariation analysis could now be examined in detail - i.e., gestation, age at maturity, and life span; and, as well, the database on variation (223 species) would be much larger than that used in covariation (81 species).

Analyses performed in section A found that systematic variation was more obvious at the family level than at the order or genus level; therefore, this analysis will concentrate at this level. All life-history traits except mode of reproduction were log-transformed as described in section A. Ecological categories consisted of 3 groups:

two specialists and a generalist, and described diet, habitat (benthic vs. pelagic dwellers), region (northern vs. southern dwellers), and zone (inshore vs. offshore dwellers). Mode of reproduction, although a life-history trait, will be used as an important covariate to examine life-history variation according to how sharks reproduce.

1. Univariate and bivariate analysis of life-history traits, mode of reproduction, and ecology

I entered the data on life-history traits as dependent variables, mode of reproduction and ecological categories as independent variables into individual one-way ANOVAs to examine variation in life-history traits. The life-history traits used were: length (size), length at maturity, birth length, fecundity, gestation period, age at maturity, life span. The ecological variables used were: diet, habitat, zone, and region. These analyses were restricted to families with 4 or more species.

2. Allometric relationship of size with mode of reproduction and ecology

The functional relationships of size with mode of reproduction and ecology were examined using one-way ANOVAs with size as the dependent variable and the categorical variables as independent variables using data on 223 species from 11 families. Bartlett's test of homogeneity and Scheffe's multiple range test of means were used in all analyses involving the ecological

categories to pinpoint differences within the 3 groups comprising each category.

3. The effects of mode of reproduction and ecology on life-history variation

To examine the effects of diet, habitat, zone, region, and mode of reproduction on each life-history trait, after removal of size effects, I compared standardized residuals from the allometric curve (i.e., residuals from the least squares regression divided by their standard deviation) among families, ecological groups, and mode of reproduction. The data were entered, separately for each life-history trait, into a one-way analysis of variance followed by a priori "t" tests using families with four or more species (according to Wooton, 1987). The categorical variables form the classes with the standardized residuals being the dependent variables.

I also compared ecological groups and mode of reproduction after removing the effects of size and family. Taking each life-history trait one at a time, I regressed that life-history trait on size for each family and pooled together the standardized residuals of each trait from all regressions. I then compared these family-adjusted residuals from different ecological groups and mode of reproduction categories using factorial ANOVAs followed by a priori "t" tests (Wooton, 1987). Similarly, I determined if any differences among families resulted from

differences in ecology and mode of reproduction after removal of size effects. I compared standardized residuals among families after adjusting for ecology and mode of reproduction differences on a trait-by-trait analysis (Wooton, 1987).

Results

1.0 Univariate and bivariate analysis

Because it has been previously established that variation in life-history was most systematic at the family level, further analyses were restricted to this taxonomic level. Eleven families containing four or more species were used in the detailed analysis. A summary of mean life-history traits are presented in Table 22. Table 23 summarizes the frequencies of occurrence within the 11 families. Individual life-history traits were entered into single one-way ANOVAs to test for differences among family, mode of reproduction, and ecology categories. For most grouping criteria, there were significant differences among means for each life-history trait (Table 23). Species which differed in mode of reproduction, ecological grouping, or family were likely to differ in life-history traits as well.

2.0 Allometric relationship of size with mode of reproduction and ecology

Mean lengths of sharks were calculated for species occupying various ecological categories and the mode of reproduction used (Table 24). All data on length were entered into one-way ANOVAs to test for significant differences in the size of sharks among the ecological categories and mode of reproduction (Table 25). Because all four ecological categories contained two 'specialists' groups and a 'generalist' group, variances associated with each category were tested to determine if one group was more variable than the other using Bartlett's test of homogeneity of variance (Table 26).

Sharks that are benthic habitat specialists were significantly smaller than pelagic habitat specialists ($P < .05$). Sharks that occupy both types of habitats were significantly different in size being intermediate between the two specialists ($P < .05$) (Tables 24 and 25). This latter group had a higher variance than the other two groups suggesting that they extend into the size range of each type of more habitat specialized sharks ($P < .05$) (Table 26). Sharks living in offshore areas were significantly smaller than inshore dwellers, with those generalists sharks that occupy both areas being significantly larger than either of the two specialists ($P < .05$) (Tables 24 and 25). However, although the variances associated with the generalist group were higher, no significant difference was

detected ($P > .05$) (Table 26). Significant diet differences in the three groups of sharks were found with sharks whose diet consisted mainly of bottom invertebrates and some small fish. These sharks were significantly smaller than sharks whose diet consisted mainly of fish and those sharks with an omnivorous type of diet ($P < .05$) (Tables 24 and 25). However, there was no significant difference in the mean size of the latter two groups ($P > .05$), although the variances of the three groups were found to be significantly different ($P < .05$). Sharks with large fish diets and those with omnivorous diets showed very little variability in size unlike the smaller sharks (Table 24). Sharks found in either the northern regions or the southern regions were not significantly different in size ($P > .05$); however, sharks that ranged into both areas (cosmopolitan) were significantly larger than both specialists groups ($P < .05$) (Tables 24 and 25). This generalist group was more variable in size than the two other groups ($P < .05$) (Table 26). Mode of reproduction in sharks appeared to be size related with oviparous sharks being significantly smaller than viviparous sharks ($P < .05$) (Table 24).

2.1 Summary of results

In general, small sharks tend to be benthic-dwellers, located offshore, feeding on bottom invertebrates and small fish, distributed in both northern and southern regions and, generally, are oviparous in their mode of reproduction. Larger sharks, in

general, tend to be more diverse in habitat, zone, diet, and region distribution and are generally viviparous. Ecology and mode of reproduction appeared related.

3.0 The effects of mode of reproduction and ecology on life-history variation

All data on length at maturity, birth length, fecundity, gestation period, age at maturity, and life span were entered individually into one-way ANOVAs to examine mean trait differences in ecological categories and mode of reproduction (Table 24). Because a functional relationship exists between size and mode of reproduction and ecology, the analysis of other life-history traits were performed with the effects of size removed. Scheffe's multiple range tests of means were used to detect differences among families, ecological groups and mode of reproduction in examination of standardized residuals after size effects had been removed ($\alpha = .05$) (Table 25).

3.1 Length at maturity

Within each category of ecology or mode of reproduction, there was no significant difference in mean length at maturity of sharks with size effects in the model ($P > .05$) (Tables 24 and 25). Among families, mode of reproduction, and ecological categories, there were no significant differences in the standardized residuals after removing the effects of size

($P > .05$) (Table 27). After removal of family effects, there was still no significant variation in length at maturity within mode of reproduction or the ecology categories ($P > .05$) (Table 28). After adjusting for the effects of each ecology category, mode of reproduction, and comparing standardized residuals among families, again, there were no significant differences detected ($P > .05$) (Table 29). Length at maturity in sharks did not seem to be affected by mode of reproduction or any ecological variables examined.

3.2 Birth length

Prior to removal of size, significant differences in birth length existed only among region groups and mode of reproduction ($P < .05$) (Tables 24 and 25). Analysis of standardized residuals, with effects of size removed, revealed a significant difference among families, mode of reproduction, and region groups ($P < .05$) but no difference among diet groups, habitat groups, and zone groups ($P > .05$) (Table 27). Size at birth differed significantly among several families ($P < .05$). Oviparous sharks gave birth to significantly smaller offspring than viviparous species ($P < .05$). Sharks distributed in northern regions have significantly smaller offspring than those distributed in southern regions and cosmopolitan waters ($P < .05$). Oviparous species give birth to significantly smaller young than viviparous species ($P < .05$).

After removing the effects of families, there were no significant differences in birth length among mode of reproduction, diet, habitat, and zone groups ($P > .05$) (Table 28). However, deviations in birth length from the allometric curve still remained within region groups after removal of family effects ($P < .05$). After adjusting for mode of reproduction and each ecology group differences, the comparison among families showed that all groups deviated significantly from the allometric curve ($P < .05$) (Table 29).

3.3 Fecundity

Before size effects were removed, significant differences in fecundity only existed within the mode of reproduction category ($P < .05$) but none within each ecological group (Tables 24 and 25). After removal of size effects, there was still significant variation among families and mode of reproduction ($P < .05$) but not among any of the ecological groups ($P > .05$) (Table 27). Mean fecundity estimates varied significantly among families ($P < .05$). Oviparous species had a significantly lower fecundity than viviparous species ($P < .05$).

After removal of family effects, there was still no significant variation explained by the ecological groups resulting from analysis of standardized residuals ($P > .05$) (Table 28).

Removal of family resulted in removal of the only degree of freedom associated with mode of reproduction; consequently, no analysis could be performed.

Comparisons among families after adjusting for the effects of mode of reproduction and ecological group differences showed that there was significant difference in all standardized residuals ($P < .05$) (Table 29). Variability associated with fecundity seemed to be related more to variation at the family level and mode of reproduction than to any ecological variable.

3.4 Gestation period

Before removal of size effects, significant differences in gestation period were detected among zone groups, region groups, and mode of reproduction ($P < .05$) (Tables 24 and 25). After adjusting for size effects, analyses of standardized residuals among six families and ecological groups showed a significant variation among families, mode of reproduction, region groups, and zone groups ($P < .05$). There was no significant variation among diet groups and habitat groups ($P > .05$) (Table 27). Average gestation periods varied significantly among families for which data were available (Table 24). Sharks distributed in the southern regions had a significantly shorter gestation period than cosmopolitan-distributed sharks ($P < .05$) but no difference existed with northern regions ($P > .05$). As well, sharks located offshore had significantly longer mean gestation periods than

inshore dwellers and oceanic dwellers ($P < .05$) (Tables 24 and 25). Oviparous species had significantly shorter gestation periods than viviparous species ($P < .05$) (Tables 24 and 25).

After removal of family differences in standardized residuals, significant variation still remained among zone groups for gestation period ($P < .05$) but regional variation was no longer significant ($P > .05$). There were still no significant differences among the other ecological groups ($P > .05$) (Table 28). There was significant variation among families in the standardized residuals after adjusting for ecology groups and mode of reproduction differences ($P < .05$) (Table 29).

3.5 Age at maturity

Prior to removal of the effects of size, significant variation in age at maturity was found in the analyses with zone groups, region groups, and mode of reproduction for species for which there is data ($P < .05$) (Tables 24 and 25). Analyses were restricted to 4 families (Table 21). Significant deviations in the standardized residuals, after removal of size effects, was recorded among families, region groups, and zone groups ($P < .05$) but not among diet or habitat groups ($P > .05$) (Table 27). Among families, age at maturity varied significantly ($P < .05$). Sharks distributed in northern regions matured at a significantly younger age than southern-distributed sharks ($P < .05$), but no differences were recorded with cosmopolitan sharks ($P > .05$). Inshore

dwellers matured significantly younger than oceanic dwellers ($P < .05$); however, no data were available on offshore dwellers. Insufficient data prevented an analysis on the effect of mode of reproduction. After removing the effects of family differences, variation in standardized residuals became insignificant ($P > .05$) (Table 28).

When differences attributed to ecology groups were adjusted, comparison among families showed significant variation in age at maturity ($P < .05$) except for habitat-specific deviations ($P > .05$) (Table 29). Age at maturity appeared to be strongly influenced only by family-level effects.

3.6 Life span

Before size effects were removed, no significant variation in life span was detected among ecology groups for which data were available ($P > .05$) (Tables 24 and 25). The analysis was restricted to three families (Table 21). There were no significant differences in standardized residuals among families or ecological groups after removal of size effects ($P > .05$) (Table 27). After adjusting for family differences and ecological differences, no significant variation in life span was detected ($P > .05$) (Tables 28 and 29). Based on the limited amount of data, variability in life span does not seem to be accounted for by family-level taxonomy or ecology. Insufficient data prevented an analysis of the effect of mode of reproduction.

3.7 Summary of results

Does occupation of various ecological regimes help shape life-history variation? The answer is yes. Ecological regimes and mode of reproduction appeared to be functionally related to size in sharks. Removal of size effects resulted in significant variation explained at the family level and/or mode of reproduction category in length at maturity (family only), birth length, fecundity, gestation, and age at maturity (family only) but not life span.

Removal of size and family effects resulted in significant variation remaining in birth length with region and gestation period with zone. The high significant values calculated for differences among regions ($P = .0102$) for birth length and for differences among zones ($P = .0035$) for gestation should rule out a suggestion that these significances arose by chance. Adjusting for ecological and mode of reproduction differences did not eliminate the differences between families.

These results suggest that size, phylogeny, and mode of reproduction strongly impact on most life-history traits. Species distribution (regions) may have contributed to shaping life-history variation in birth length. Distribution by zones may have contributed to shaping life-history variation in gestation period. Several of the ecological correlates suggest phylogenetic lineages differ in their expressions of some of these traits.

Discussion

The discussion centres on the relationship of size, phylogeny, mode of reproduction, and ecology to shark life-histories. Overall conclusions were based on univariate, bivariate, and multivariate analysis. Limitations on the available data in terms of partial data on some species and no data at all in many others limit the generality of these conclusions.

Allometry

In sharks, all life-history traits, with the exception of gestation period, were scaled to body size. Correlations with size had a strong impact on length at maturity, birth length, fecundity, age at maturity, and life span accounting for, on the average, 41% of the variation in a trait. This result is consistent with other allometric studies of life-histories in mammals (Stearns, 1983; Gittleman, 1986; Harvey and Clutton-Brock, 1985), reptiles (Stearns, 1984; Dunham and Miles, 1985), salmonids (Hutchings and Morris, 1985), and birds (Zammuto, 1986; Murphy, 1989). Whether size alone, size and other variables which covary with size, or something else which happens to covary with size, exerts a causal effect on life-histories cannot be distinguished from this type of analysis (Harvey and Clutton-Brock, 1985). Most life-history traits were found to be interrelated; thus, causal effects would be complex to interpret.

Phylogenetic effects

The nested analyses of variance used in this study with and without the regression on length (allometric relationships) examined how the total variation in life-history traits was distributed across taxonomic levels, assuming that taxonomy reflects phylogeny. This comparative method allows for the disentanglement of the separate influences of size and phylogeny in closely-related species by partitioning the variance between taxa in order to distinguish the effects attributed to ancestry.

In the nested ANOVAs, significant variation was found at the order and family levels in length, length at maturity, birth length, fecundity, and gestation period with family differences being more variable than order differences. After size effects were removed at the family level, these significant differences remained. These family level differences are assumed to represent phylogenetic history - i.e., "ghosts" of past adaptations. Dunham and Miles (1985) reached similar conclusions in reptiles, as did Stearns (1983) in his work on mammals. Because most of the variance was attributed to family level, this suggests that further tests of life-history hypotheses be made at this level. Pagel and Harvey (1988) argued that choosing a higher taxonomic level than species would reduce the likelihood of taxonomic artifacts influencing comparative trends. Lauder (1982) and Harvey and Clutton-Brock (1985) suggest, lower levels may need to be considered as well. In sharks, there was significant variation found at the genus level; but it appears less influential than familial level variation.

However, this replication of the comparative trend at the genus level is further assurance that the relationship seen at the family and order levels was not due to taxonomic artifacts (Pagel and Harvey, 1988).

Interrelationship of life-history traits

Three patterns emerged in the correlation matrix of life-history traits. First, all size traits - i.e., length, length at maturity and birth length - were all highly positively correlated with all other traits, except with gestation period. Birth length was weakly correlated with fecundity. Second, fecundity, a reproductive component, only showed strong positive correlations with length and the two age variables. Gestation, another reproductive component, showed no relationship with other life-history traits. Third, both age variables - i.e., age at maturity and life span - were significantly and positively correlated with all the length-based traits and with each other.

Some interrelationships of life-history traits changed considerably when the effects of size were removed. Length at maturity was still positively correlated with birth length and age at maturity in sharks. Fecundity was inversely correlated with birth length, suggesting a trade-off between number and size of offspring and that this relationship was masked by the effects of length. Schaeffer (1974) argued that environmental variability, which impacts on juvenile mortality, favored reduced reproductive effort, smaller clutches, and longer-lived organisms. But if this variability affects adult

survival, increased reproductive effort, larger clutches, and short-lived organisms would be favored. Holden (1974) suggested that the mortality rate of sharks producing large numbers of young is higher in the early years of life than in those species producing smaller litters, especially as the size of the young is inversely related to litter size. Although the inverse relationship of fecundity and birth length was shown, cost of reproduction in terms of survival did not appear to be present in that no correlations were found between fecundity and life span in this analysis. If fecundity was a major cost of reproduction in that it reduces survival, as it is thought to be in birds (Murphy, 1989), it should vary inversely with life span - i.e., large litter size with shorter life span and vice-versa. In sharks, this relationship may be confounded by the two modes of reproduction because larger sharks are generally viviparous and produce larger young than oviparous species which tend to be small and have low fecundity and smaller young. Finally, the relationship between age at maturity and longevity may not depend upon body size among species of sharks. A conclusion similar to that was reached in mammalian studies (Harvey and Zammuto, 1985). The interrelationship of life-history traits in sharks is a complex one, influenced by body size and possibly mode of reproduction. Thus, it is well established that body size is of central importance in shark evolution and it becomes necessary to explore patterns of covariation in life-history traits.

Covariation of life-history traits

Stearns (1980) posed the question, "Is the perception of a tactic a function of the taxonomic units used?" and made the case for comparative studies at higher taxonomic levels rather than at the intraspecific level (Stearns, 1980, 1983, 1984). Covariation among traits measured across species can arise as a result of common ancestry and from convergent or parallel evolution (Pagel and Harvey, 1988). Although the nested ANOVAs suggested that further analysis of life-histories be conducted at the family level, the analysis of covariation also considered genus-level effects. It was felt that, although sample size is decreased and some extra information is incorporated, the analysis solely on family could ignore large amounts of inter-genus variation in some life-history traits (Harvey and Clutton-Brock, 1985).

Principal component analyses defined a size component which ordered species from small sharks, maturing at a small size, low fecundity, and small offspring to large sharks, maturing at a larger size, high fecundity, and large offspring. Significant variation in the second principal component described a second axis consisting of many small offspring versus few large offspring indicating life-history traits covary along more than one significant dimension. These two dimensions represent the patterns of covariation of life-history traits expected from r/K selection theory (Stearns, 1976, 1977). Removal of phylogenetic effects of family and genus had little effect on the pattern of covariation. This indicates that the dominant patterns in life-history evolution are the same in all lineages.

Size explained most of the covariation seen in life-history traits and as Stearns (1984) asserts, it is the reason for the continuum. The pattern is due to the shared correlation of size with the other life-history traits, except fecundity and birth length. Removal of size and the phylogenetic effects of family and genus weaken the patterns associated with r/K selection by removing all shared correlations with size and changing the polarity of the first principal component in a manner similar to the one reported by Stearns (1984) for reptiles. Again, the dominant pattern was the same for all lineages. Size is a central feature in the pattern of covariation followed by the fecundity-birth length relationship across taxa. In the analysis within families, removal of size effect showed some differences among lineages with the amount of variation varying in PC1. Squalidae and Carcharhinidae are the only families to show the pattern of the first principal component after removal of size effects. However, both of these families are numerically over-represented (29 species) in the raw data on the 81 species which may result in this pattern dominating the PC1 regardless of how much inter-family differences there are. This close association of across and within family phylogeny, nevertheless, suggests that life-history covariation is lineage dependent and there are strong effects of morphological features upon life-histories in sharks similar to results found in Salmonids (Hutchings and Morris, 1985). However, within Carcharhinidae, after removal of residual effects of length and family, there were no significant variations attributed to genus level, thus, not supporting the idea of lineage-dependency at this more finely split level.

Size has the greatest impact on covariation of life-history traits; whereas, phylogeny seems to play a lesser role. Much of the differences among families of sharks can be accounted for by correlations with size. Although phylogeny accounts for the smallest variability in constraining shark life-histories, its effects cannot be ignored, a similar conclusion reached by Stearns (1983, 1984) and Dunham and Miles (1985). Perception of covariation among life-history traits thought to be a function of r/K selection was dependent on taxonomic level and can be accounted for by correlation with size (Stearns 1983, 1984). The concept of r/K selection in this study is only used in a comparative sense since, in sharks, species are not distributed at opposite end points but along the two continuums described by the pattern of covariation. A species position on the continuum will be a function of selective factors, operating spatially and temporally in a compromise between the demands of reproduction and survival. The observed tactic - i.e., pattern of covariation - is assumed to accurately reflect the selection pressures of sharks habitat. Most traits in sharks appear to be constrained along phylogenetic trends with a significant amount of the covariation depending thus far on body size. Are there any other significant correlates which effect these patterns of covariation in sharks?

Mode of reproduction

Dunham and Miles (1985) suggested that the axis of life-history variation could be partitioned according to mode of reproduction and brood frequency. They proposed, in their studies of reptiles, that

separate axes could describe life-history variation in lizards and snakes. The authors found significant order (lizards vs. snakes) variations in life-history traits even after the removal of size and they interpret these results as an absence of strong phylogenetic effects - i.e., common ancestry. In sharks, significant family variation existed for length at maturity, birth length, fecundity, and gestation after the removal of size. In the analysis of mode of reproduction, these significant family variations were the same ones found in the 189 viviparous species within 17 families; however, only significant family variation was seen in fecundity in the 58 oviparous species belonging to 5 families. Patterns of covariation of life-history traits in viviparous species matched the overall pattern; however, such was not the case for oviparous species even after factoring out phylogenetic effects. Mode of reproduction is not a familial diagnostic character since phylogenetic systematics in sharks is based solely on skeletal structures and not on any life-history attributes. Similarities among families of sharks may not entirely be accounted for by shared ancestry, but may also be influenced by physiological constraints of mode of reproduction, particularly relating to fecundity. Wourms (1977) argues that oviparity in sharks is considered to be the least specialized mode of reproduction with the production of a small number of large eggs being selected and that viviparity has evolved independently in different major groups of sharks and other elasmobranchs. Evolution of mode of reproduction may be continuing toward viviparity because two of the families, Proscylliidae and Scyliorhinidae, have a mixture of both modes (Wourms 1977). Oviparity is found almost exclusively in orders

Orectolobiformes and Heterodontiformes, while four orders are all viviparous and 2 orders, Lamniformes and Carcharhiniformes, have 1 family each that is oviparous. Within the order Rajiformes, skates, rays, and chimeras, derived from shark-like ancestors, only skates have retained oviparity. The other four suborders are viviparous (Wourms, 1977). Ginglymostoma, nurse sharks, a genus belonging to Orectolobiformes, are considered to have made the transition from oviparity to viviparity only recently (Gudger, 1940). In life-history studies, careful attention needs to be paid to mode of reproduction and its influence on patterns of covariation in life-history traits.

Ecology

The analysis of habitat, diet, zone, and region effects on the patterns of covariation after phylogenetic (family) effects had been removed indicated that specific ecological factors may have some influences on these patterns. Dietetic and habitat differences were detected and may be important factors to be considered in shaping life-history evolution of sharks. Given the available knowledge of shark ecology, it would be hard to discuss these possible sources of selective forces without looking at their relationship with size and mode of reproduction. Tortonese (1950) first suggested that differences in ecology of sharks may be associated with difference in size and mode of reproduction. He noted that, in general, oviparous species were benthic, littoral, and of small size while viviparious species were more diverse in size and habitat. Wourms (1977) noted that feeding ecology was also a function of size and habitat; large

sharks are active predators, pelagic in nature, such as the Carcharhinids and Lammids, and tend to be viviparous. Smaller sharks, such as Heterodontids and Scyliorhinids, are more sedentary, feeding on benthic invertebrates and small fishes, and tend to be oviparous. The pattern of covariation in life-history traits in sharks describe tactics that are presumed to be adaptive responses and reflect selection pressures of habitat. Neither diet nor habitat are invariant diagnostic characteristics of families of sharks. Sharks are typically habitat generalists - i.e., habitat in the wide sense of the meaning, occuring over wide geographical areas (Smith, 1986) - and this adds to the difficulty of separating the influences of size and ecology in this type of broad interspecific analyses.

Life-history variation and ecology

The previous discussion has shown that size, phylogeny, and mode of reproduction are important covariates and must be taken into account before most theories of life-history evolution in sharks can be tested. There is also some suggestion that ecological factors may influence the pattern of covariation as expected from life-history theory. Through ecological based comparisons, it should be possible to account for the importance of micro-evolutionary processes in shaping life-history variation within lineages (Barbault, 1988). At various taxonomic levels of life-history, variability has been linked to specific ecological factors such as foraging (Dunham and Miles, 1985). Body size in sharks appears to be closely related to ecological differences. Similar results were reported for primates (Harvey and Clutton-Brock,

1985). Mode of reproduction also appears to be a function of size with oviparous species in the families Heterodontidae, Proscylliidae, and Scyliorhinidae being smaller than most viviparous species in other families, with a notable exception of Squalidae. Tortonese (1950) noted that viviparity was a function of large adult size in sharks; an exception to this may be whale shark, Rhiniodon typus, approximately 2000 cm in length, which is thought to be oviparous. In the continuing discussion, mode of reproduction, a life-history trait, will be used as a covariate and analyses of individual life-history traits will consider its effects as well as those of phylogeny and ecology.

Upon removal of size effects, significant variation was seen in birth length, fecundity, gestation, and age at maturity in relation to family, mode of reproduction, and various ecological factors. These may be attributed more to taxonomic associations because, with removal of phylogenetic effects, significant variation vanishes in mode of reproduction and most ecological categories. This taxonomic variation probably reflects the evolutionary history of the groups rather than ecology (Harvey and Clutton-Brock, 1985). However, a few significant ecological associations were observed and cannot be ignored. Variation in birth length associated with region and variation in gestation associated with inshore-offshore zones remained. Species of sharks inhabiting northern waters, such as several members of Squalidae and Scyliorhinidae, give birth to smaller young than those species inhabiting southern waters - e.g., Hexanchids - or those more cosmopolitan in distribution, such as the Carcharhinids. Species of sharks inhabiting mostly inshore waters generally have shorter

gestation periods, as seen in some members of the Heterodontidae and Sphyrinidae families. On the other hand, species which range more offshore, such as Squalids, have longer gestation periods than inshore-offshore (oceanic) dwellers, such as Carcharhinids and Triakids. Many species of sharks live offshore and may come inshore to find food, give birth, or in response to yet-undefined needs (Springer, 1976) and this contributes to the complexity of separating influences.

These ecological associations, independent of size and phylogeny, may be adaptive responses; but it is worthwhile noting that, in most families, clear geographic barriers do not exist with respect to region and zone. However, interspecific comparisons may hide the results of ecologically related natural selection which may be only found by doing intraspecific life-history comparisons (Wooton, 1987). It is hard to evaluate whether the coarseness of the ecological categories used in the analysis obscures adaptive differences. Whether or not ecological differences found here are independent of other ecological factors is also not known.

After adjusting for mode of reproduction and ecological differences, significant variation in birth length, fecundity, gestation, and age at maturity remained among families similar to findings without adjustment. Most families contain species belonging to a wide range of ecological settings in which there is a mixture within each ecological category of specialists and generalists. Total variation in family analysis could be explained by variation within families suggesting a strong effect of phylogenetic position attributed

to differences among ancestors (Bell, 1989) rather than an effect of ecology or mode of reproduction. Alternatively, as Wooton (1987) suggests, these differences might be adaptive responses to ecological or behavioural factors unrelated to the variables studied.

Absence of other ecological adaptions at the family level may be related to the fact that the prime ecological adaption may be body size or that it occurs within lower taxonomic levels. Gittleman (1986) found that, at the family level in carnivores, most life-history traits did not correlate with ecological factors although some dietetic differences did exist in some families. Wooton (1987) determined that ecological factors appeared to have little effect on evolution of age at first reproduction in mammals.

The comparative method

In section A, the comparative method was based on the nested analysis of variance which relied on inferences from statistical patterns to control for phylogeny (Harvey and Mace 1982, Stearns 1983, Bell 1989). The components of variance at any given level of taxonomy are thought to represent phylogenetic effects attributable to differences among ancestors (Bell, 1989). Although, as Pagel and Harvey (1988) argue, the nested ANOVA may not remove phylogenetic effects with as much certainty, this method has the advantage of being widely applicable to real data sets. The other criticism of this method is that the results of across-taxa comparison may be biased by species-rich taxa (Pagel and Harvey, 1988). In my analysis, I have

used within-taxa analysis of patterns to control for this. The nested ANOVA enables an examination of how the total variation in a character is distributed across taxonomic levels and the level which contributes most of the variance of the dependent variable is the level at which to concentrate the analysis according to Clutton-Brock and Harvey (1979) and Harvey and Clutton-Brock (1985). In section B, life-history variation, variability in a trait that was associated with phylogenetic groupings - i.e., family, in this case - was removed directly by regression techniques. The protocol used was that employed by Wooton (1987) in a similar approach to remove order effects in a study of mammalian age at first reproduction.

Another area that has received a lot of attention is the appropriate use of regression models in the comparative method. In all of the analyses used in my study of sharks, I chose the least-squares regression model - i.e., Model 1. Although this regression line underestimates the true slope, it is the only line-fitting method that creates deviation scores that are completely uncorrelated with the x variable - i.e., body size (Pagel and Harvey, 1988). These deviation scores which represent the removal of the confounding variate, body size, prior to hypothesis testing, were used as independent points in principal component analyses. Because the focus of the analyses was on size specific deviations in life-history traits from the allometric curve, deviations from the line perpendicular to the x axis least squares seemed to be the appropriate model to minimize these deviations (Wooton, 1987) and were used exclusively in both sections.

The proper choice of statistical technique will depend on what the investigator is interested in doing. If one is interested in trying to remove, control, or estimate phylogenetic effects, a nested ANOVA is usually the choice (Pagel and Harvey, 1988; Bell, 1989). If one wants to test functional relationships, analysis of covariance may be a better choice (Pagel and Harvey, 1988; Bell, 1989). However, although both methods introduce statistical rigor, there are some disadvantages associated with the choice of either or both methods (see Pagel and Harvey, 1988, and Bell, 1989, for excellent reviews of the comparative methods).

Relevance to other work on sharks

The analyses presented here places the data in a framework to study questions on quantitative traits of sharks. With the exception of gestation periods, all life history traits are interrelated in allometric relationships or tradeoffs. Allometric relationships were found in size-birth, size-maturity, size-lifespan, size-mode of reproduction, and size-fecundity. Gestation period was not correlated with fecundity or any other trait and from the ecological analysis it appears to be influenced by residency inshore or offshore, being shorter in the former and probably environmentally controlled.

The available literature on extensive studies of shark life histories is extremely poor. The two main works, Tortonese (1950) and Wourms (1977) focused on reproductive strategies in sharks. Tortonese (1950) was the first to suggest any possible relationship between

habitat and reproductive strategies with oviparous sharks being smaller benthic dwellers and viviparous sharks being larger and more diverse in habitat. Both Tortonese (1950) and Wourms (1977) recognized that body size played a central role in life histories and that oviparity and viviparity were two extremes in a continuum of reproductive adaptations (Wourms 1977). The analyses presented here substantiates these trends and places emphasis on body size, mode of reproduction, phylogeny, and ecology as covariates shaping life histories of sharks.

Summary and conclusions

This comparative study examined interspecific variation in seven life-history traits across the Euselachiians, the modern sharks. The primary goal was to determine the relative importance of size, phylogeny, and ecology on patterns of covariation in life-history as well as variation in individual life-history traits. Body size emerged as the primary cause of existing variability and most traits were also constrained along phylogenetic trends in a lineage dependent fashion. Patterns of covariation of life traits - i.e., tactics - show that sharks covary significantly along two dimensions and the pattern was dominant across species, genus, and family levels and also within family taxa. This grouping of life-history traits into "tactics" at these three levels were found to be influenced predominately by size and, to a lesser extent, phylogeny. Removal of size and phylogeny weaken the pattern perceived to be predicted by r/K selection theory.

Mode of reproduction was identified as another important covariate; however, its influence on patterns of covariation seems to be tied closely to body size in sharks. It appears that size is important in selection for alternative mode of reproduction, in terms of development strategies. The coadaptive consequences of large body size, assumed to be a function of competition, seem to account for differences in mode of reproduction in sharks and probably in other existing Chondrichthyans. This suggests that in closely-related organisms that exhibit oviparity and viviparity, the axis of covariation may have to be defined according to how a species reproduces.

Dietetic and habitat differences may also have some influences on the pattern of covariation in life-histories of sharks. However, the role these ecological specific selection pressures may have on the observed covariation of traits or how they defined a species position along the two gradients is difficult to interpret. It appears that these ecological differences are probably entangled with the influences of size and, consequently, mode of reproduction even after the removal of phylogenetic effects. As well, two ecological associations were found in the analyses of variation in individual life-history traits: region distribution with birth length and inshore-offshore zone distribution with gestation period. Other ecological factors appeared to have little effect on the evolution of life-history traits, probably due to constraints imposed by size, phylogeny, and mode of reproduction. Lack of data on species with certain combinations of ecological traits would also attribute to lack of ecological

associations with life-history traits. It may be argued that ecological associations demonstrated here are, in reality, taxonomic associations in that those differences detected arose from differences among ancestors through selection operating in the past (Bell, 1989). Differences in life-histories of sharks at the family level are difficult to interpret in a meaningful way and could have arisen from ecological selection pressures or phylogenetic constraints. However, some significant ecological associations were observed compared with the total number of trends examined in life-history variation; and they represent trends that should be considered in further studies of life histories (Gittleman, 1986).

This study has shown that covariation of life-history traits, defined here as tactics, exists at higher taxonomic levels and are constrained by body size and phylogeny in one of the oldest jawed vertebrates. Most of the recent work in this area has been on "new," in the geological time sense, taxonomic groups such as birds, teleosts, carnivores, mammals, and other primates. Life-history variation and covariation of sharks is also influenced, in part, by mode of reproduction and ecology. Sharks offer a unique opportunity to analyze life-history evolution under extremely diverse ecological and historical situations. Life-history studies of sharks can be helpful in answering some fundamental questions about evolution. Outside of the strong relationships between size and the other life-history traits, natural selection also favors the co-occurrence of particular sets of life-history traits such as fecundity and birth length. This inverse relationship is an important prediction from r/K selection

theory involving the trade-off between many small and few large offspring. Reproduction is the central focal point in life-history studies and evolution of strategies. Size, number of offspring, gestation period, fecundity, and mode of reproduction are all sources of life-history variation. Other aspects of reproduction such as energy resource allocation to embryos, nutrition, and brood frequency need to be examined when more data are available. Whether natural selection favors the existence of certain life-history traits within certain environments should probably be addressed more on an intraspecific level to determine ecological selection pressures.

Future studies should consider further the limits of mode of reproduction due to allometric and physiological constraints. Ecological selection pressures may be more demonstrative using intraspecific studies. More detailed intraspecific data are needed to be collected - in particular, body weight, growth, age at maturity, life span, gestation, brood frequency, dispersal and migration, mode of reproduction, and parental care as well as accurate information on ecological factors. Many of the interesting species of sharks such as Cetorhinids, Chlamydoselachids, Rhiniodontids, and Megachasmids were not included due to lack of data. The comparative method, while focusing on generating hypothesis about evolution, was also useful in suggesting the kinds of attributes and ecological associations that could be used in detailed intraspecific studies of life histories in sharks.

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Table 1. Mean values of traits for 4 orders, 16 families (228 species): Mode of reproduction coded as : 0 = oviparous, 1 = viviparous, and 0+1 for a mixture of both types. Trait measurements in parenthesis are actual values for 1 species (no average possible).

Order/Family	N	Length (cm)		Length at maturity (cm)		Birth length (cm)		Fecundity (#)		Gestation (months)		Age at maturity (yrs)		Life span (yrs)		Mode of reproduction
		x	S.D.	x	S.D.	x	S.D.	x	S.D.	x	S.D.	x	S.D.	x	S.D.	Code
Squaliformes	54	103.6	86.1	68.1	35.2	26.6	12.9	9.1	7.1	20.3	5.7	(16.5)	-	(27.5)	-	1
Echinorhinidae	2	249.0	38.9	-	-	52.3	10.3	(19.5)	-	-	-	-	-	-	-	1
Squalidae	49	97.1	84.6	69.0	35.8	24.9	10.4	8.9	7.2	20.3	5.7	(16.5)	-	27.5	-	1
Oxynotidae	3	113.3	39.2	(50.0)	-	17.5	10.6	7.6	0.4	-	-	-	-	-	-	1
Orectolobiformes	14	125.6	83.4	(235.0)	-	25.3	9.3	23.2	14.5	-	-	-	-	(25.0)	-	0+1
Parascyllidae	4	62.3	21.9	-	-	(17.0)	-	-	-	-	-	-	-	-	-	0+1
Orectolobidae	3	181.7	99.1	-	-	20.5	0.7	(37.0)	-	-	-	-	-	-	-	1
Hemiscyllidae	5	89.0	18.6	-	-	-	-	-	-	-	-	-	-	-	-	0
Ginglymostomatidae	2	259.5	0.7	(235.0)	-	34.3	8.1	16.3	11.7	-	-	-	-	(25.0)	-	1
Lamniformes	11	412.4	145.6	300.9	44.7	98.1	21.7	5.6	4.7	8.5	0.5	6.3	1.3	28.9	19.4	1
Odontaspididae	3	328.7	30.1	(260.0)	-	102.5	3.5	6.3	6.0	(8.5)	-	-	-	-	-	1
Alopiidae	3	470.8	179.0	325.2	42.1	105.2	25.9	3.0	1.0	(9.0)	-	(7.5)	-	(50.0)	-	1
Lamnidae	5	427.6	168.6	(269.0)	-	90.5	25.7	6.8	5.8	(8.0)	-	5.8	1.1	18.4	9.3	1
Carcharhiniformes	149	120.6	91.4	107.2	70.7	35.5	20.1	9.2	14.8	10.6	2.3	4.6	2.8	16.7	8.0	0+1
Proscylliidae	6	50.0	27.5	26.8	10.8	12.3	3.2	2.0	0.0	-	-	-	-	-	-	0+1
Triakidae	32	119.8	41.1	83.8	29.2	28.3	7.0	9.3	5.4	10.9	1.6	4.0	3.5	15.5	9.2	1
Hemigaleidae	3	136.1	51.1	67.5	21.2	39.7	11.0	8.0	1.4	-	-	-	-	-	-	1
Carcharhinidae	40	204.9	104.9	150.5	71.2	52.6	16.9	10.6	22.9	11.4	1.8	4.9	2.5	16.9	8.2	1
Sphyrnidae	8	225.4	103.1	181.5	83.3	43.0	11.8	21.2	11.3	7.5	0.7	-	-	-	-	1
Scyliorhinidae	60	57.1	20.8	48.4	16.5	12.0	5.5	4.2	5.9	8.7	3.1	-	-	-	-	0+1

Table 2. Statistics associated with log-transformation of values of life-history traits to stabilize the variance.

Trait	N	Mean	Standard deviation	Skewness	Kurtosis
Length	228	4.6	0.7	0.3	-0.4
Length at maturity	109	4.5	0.7	0.0	-0.5
Birth length	137	3.4	0.7	-0.3	-0.5
Fecundity	144	1.8	0.9	0.5	0.0
Gestation	43	2.4	0.3	0.1	2.9
Age at maturity	23	1.5	0.7	-0.2	-0.5
Life span	20	2.8	0.6	-0.5	-0.2

Table 3. Impact of average length of adult females on life history traits. Data are log-transformed: 4 Orders, 16 families, 228 species. Least square regression model.

Trait	N	Mean[a]	r^2	Slope	Intercept	P
Length at maturity	109	109.88	.92	.93	.01	.0000
Birth length	137	37.66	.75	.80	-.47	.0000
Fecundity	144	9.20	.18	.52	-.73	.0001
Gestation	43	11.33	.00	-.02	2.48	.8098
Age at maturity	23	5.33	.28	.63	-1.90	.0101
Life span	20	19.52	.31	-.18	.55	.0109

[a]Values are raw average values.

Table 4. Pearson product moment correlation matrix for life history traits. The coefficients are based on values for 228 species. P = level of significance calculated for Ho: correlation = 0; N = number of species. Size effects included.

Trait	Length	Length at maturity	Birth length	Fecundity	Gestation	Age at maturity	Life span
Length		.9609	.8685	.4291	-.0378	.5251	.5558
P		.0001	.0001	.0001	.8098	.0101	.0109
N		109	137	144	43	23	20
Length at maturity			.8859	.4323	-.2262	.6527	.6056
P			.0001	.0001	.1847	.0010	.0060
N			84	94	36	22	19
Birth length				.1657	.1004	.4528	.5374
P				.0808	.5378	.0343	.0176
N				112	40	22	19
Fecundity					.1702	.4061	.1276
P					.2875	.0608	.5920
N					41	22	20
Gestation						.0212	.1553
P						.6048	.6125
N						15	13
Age at maturity							.8146
P							.0001
N							18
Life span							
P							
N							

Table 5. Pearson product moment correlation matrix for life history traits adjusted for size. Size effects removed by regression analysis. P = level of significance calculated for Ho: correlation = 0; N = number of species.

Trait	Length at maturity	Birth length	Fecundity	Gestation	Age at maturity	Life span
Length at maturity		.2638	-.0622	-.0652	.5414	.3259
P		.0153	.5513	.7055	.0093	.1733
N		84	94	36	22	19
Birth length			-.3648	.1290	.1299	.3074
P			.0001	.4275	.5643	.2005
N			112	40	22	19
Fecundity				.2130	.3002	-.0829
P				.1812	.1746	.7283
N				41	22	20
Gestation					.0400	.3844
P					.4747	.1947
N					15	13
Age at maturity						.7416
P						.0004
N						18
Life span						
P						
N						

Table 6. Two-level nested ANOVA for individual traits. Size effects removed by regression analysis. 4 orders, 16 families, 228 species. Number of species used in parentheses. Classification varibles are order and family nested within order.

Analysis	Order		Family (Order)		Type I SS % Variance explained by			r^2
	F	P	F	P	Order	Family	Residual	
Length effects included								
Length (228)	33.06	.0001	18.60	.0001	18	42	40	.60
Length at maturity (109)	17.12	.0001	11.05	.0001	22	37	41	.59
Birth length (137)	35.37	.0001	24.24	.0001	21	54	25	.75
Fecundity (144)	3.93	.0101	6.11	.0001	6	30	64	.36
Gestation period (43)	16.20	.0001	2.78	.0324	40	17	43	.57
Age at maturity (23)	3.05	.0725	0.36	.7021	25	3	72	.28
Life span (20)	1.10	.3472	1.14	.3472	17	12	71	.29
					x 21.29	x 27.86	x 50.86	
Length effects removed								
Length at maturity	2.65	.0533	3.48	.0014	6	21	73	.27
Birth length	0.31	.0001	4.95	.0001	12	27	61	.39
Fecundity	9.85	.0001	3.61	.0003	15	18	67	.33
Gestation period	15.31	.0001	2.93	.0260	38	18	44	.56
Age at maturity	6.58	.0072	0.02	.9787	42	0	58	.42
Life span	1.56	.2442	0.97	.4031	23	9	68	.32
					x 22.67	x 15.50	x 61.83	

Table 7. Two-level nested ANOVA for individual traits. Size effects removed by regression analysis. 6 families, 28 genera, 159 species. Number of species used in parentheses. Classification variables are family and genus nested within family.

Analysis	Family F	Family P	Genus (Family) F	Genus (Family) P	Type I SS % Variance explained by Family	Genus	Residual	r^2
Length effects included								
Length (159)	61.36	.0001	6.49	.0001	53	25	23	.77
Length at maturity (73)	28.47	.0001	4.46	.0001	50	26	24	.76
Birth length (89)	89.73	.0001	5.93	.0001	73	16	11	.89
Fecundity (95)	9.78	.0001	2.73	.0014	24	31	45	.55
Gestation period (32)	12.48	.0001	1.83	.1482	62	11	27	.73
Age at maturity (16)	3.19	.0719	0.60	.5679	46	6	48	.52
Life span (12)	0.69	.5902	0.88	.4614	21	18	61	.39
					x 47.00	x 19.00	x 34.14	
Length effects removed								
Length at maturity	2.56	.0430	2.34	.0148	12	31	57	.43
Birth length	7.72	.0001	2.69	.0025	26	29	45	.55
Fecundity	9.71	.0001	3.46	.0001	22	36	42	.58
Gestation period	11.40	.0001	1.68	.1831	60	11	29	.71
Age at maturity	5.43	.0178	0.52	.6113	60	3	47	.63
Life span	1.20	.3876	0.99	.4264	31	11	52	.48
					x 35.17	x 20.17	x 45.33	

Table 8. Principal component analysis on 4 life-history traits. Effects of size, family, and genus removed using general linear models.

Analysis	% Variance explained by PC1	PC2	PC3	Total
A. Length effects included				
81 species	75.53	21.35	2.37	99.25
81 species--family effects removed	70.41	24.41	4.00	98.52
63 species--genus effects removed	75.02	15.53	6.67	97.22
B. Length effects removed				
81 species	75.53	21.35	2.37	99.25
81 species--length effects removed	54.73	30.03	15.24	100.00
81 species--length + family effects removed	57.97	28.77	13.26	100.00
63 species--length + genus effects removed	49.49	34.33	16.18	100.00

Table 9. Unrotated component loadings for principal components 1, 2, and 3.

Analysis	Length	Length at maturity	Birth length	Fecundity
A. Principal component 1				
Length effects included				
81 species	.9846	.9786	.9071	.5208
81 species--family effects removed	.9687	.9712	.8127	.5238
63 species--genus effects removed	.9411	.9448	.7876	.7761
Length effects removed				
81 species--length effects removed		.5143	.8616	-.7970
81 species--length + family effects removed		.6115	.8815	-.7668
63 species--length + genus effects removed		.6548	.8743	-.5398
B. Principal component 2				
Length effects included				
81 species	-.0419	-.0867	-.3491	.8503
81 species--family effects removed	.0433	-.0659	-.5109	.8349
63 species--genus effects removed	.0243	-.0380	-.5438	.5687
Length effects removed				
81 species--length effects removed		.8453	-.1213	.4143
81 species--length + family effects removed		.7629	-.0724	.5252
63 species--length + genus effects removed		.6538	-.0105	.7761
C. Principal component 3				
Length effects included				
81 species	-.1115	-.1462	.2351	.0761
81 species--family effects removed	-.1802	-.1451	.2794	.1688
63 species--genus effects removed	-.2467	-.2191	.2893	.2724
Length effects removed				
81 species--length effects removed		-.1447	.4929	.4395
81 species--length + family effects removed		-.2098	.4665	.3691
63 species--length + genus effects removed		-.3792	.4853	.3260

Table 10. Changes in correlation matrices as effects of length and taxon are removed.

Analysis	Length effects included: Length at maturity	Birth length	Fecundity	Analysis	Length effects removed: Length at maturity	Birth length	Fecundity
A. 81 species				D. 81 species--length effects			
Length	.9687	.8805	.4675	Length at maturity	.2692	-.1232	
Length at maturity		.8846	.4258	Birth length		-.5203	
Birth length			.1935				
B. 81 species--family effects				E. 81 species--length + family effects			
Length	.9349	.7182	.5115	Length at maturity	.3860	-.1457	
Length at maturity		.7781	.4309	Birth length		-.5418	
Birth length			.0461				
C. 63 species--genus effects				F. 63 species--length + genus effects			
Length	.8869	.6613	.6754	Length at maturity	.3817	.0303	
Length at maturity		.6965	.6535	Birth length		-.3219	
Birth length			.3807				

Table 11. Correlation matrices of principal component scores with gestation, age at maturity, and life span. ( ) indicates the number of observations used.

Analysis	Length effects included		
	Gestation	Age at maturity	Life span
A. 81 species			
Principal component 1 scores	-.0435 (33)	.2299 (22)	.2300 (18)
Principal component 2 scores	.0796	.6071	.4723
B. 81 species--family effects			
Principal component 1 scores	.1551 (33)	.5336 (22)	.4399 (18)
Principal component 2 scores	.0829	.1072	.0417
C. 63 species--genus effects			
Principal component 1 scores	-.1293 (26)	.1726 (17)	.1351 (13)
Principal component 2 scores	.0715	-.3348	-.3151

Table 12. Principal component analysis within families. Size effects removed by regression analysis. Only families with four or more species used.

Family	N	% Variance explained by PC1	PC2	PC3	Total
Squalidae	10	75.47	16.08	8.45	100.00
Triakidae	17	47.73	33.69	18.58	100.00
Carcharhinidae	30	69.23	26.96	3.81	100.00
Sphyrnidae	5	54.56	39.78	5.66	100.00
Scyliorhinidae	7	56.56	33.33	11.11	100.00
		x = 60.51	x = 29.97	x = 9.52	

Table 13. Unrotated component loadings of the first principal component of the analysis within families.

Family	N	Length at maturity	Birth length	Fecundity
Squalidae	10	.8695	.9125	-.8217
Triakidae	17	.8507	-.2093	.8151
Carcharhinidae	30	.7462	.9681	-.7634
Sphyriniidae	5	.4824	-.9604	.6941
Scyliorhinidae	7	.9126	.9128	.0268

Table 14. Changes in correlation matrices of life-history traits, as the effects of size are removed, within families.

Family	N	Length at maturity		Birth length
		Birth length	Fecundity	Fecundity
Squalidae	10	.7276	-.5294	-.6338
Triakidae	17	-.1251	.4188	.0197
Carcharhinidae	30	.6793	-.1912	-.7017
Sphyrniidae	5	-.4628	-.1976	-.5595
Scyliorhinidae	7	.6665	.0035	.0161

Table 15. One-way ANOVA for three traits after effects of size and family have been removed using general linear models. Genera within Carcharhinidae are compared (3 genera, 24 species).

Trait	Genus		Type I SS: % Variance explained by		r^2
	F	P	Genus	Residual	
Length at maturity	1.32	.2892	11	89	.11
Birth length	2.80	.0836	21	79	.21
Fecundity	0.94	.4058	8	92	.08

Table 16. One-way ANOVA on family differences classified by mode of reproduction. Size effects removed by regression analysis.

Analysis	Family F	Family P	Type I SS % Variance explained by Family	Type I SS % Variance explained by Residual	r^2
Oviparous mode (58 species)					
Length effects included					
Length (58)	6.30	.0003	32	68	.32
Length at maturity (20)	1.55	.2407	15	85	.15
Length at birth (23)	2.78	.0859	22	78	.22
Fecundity (29)	25.35	.0001	48	52	.48
Gestation (10)	0.02	.8896	0	100	0
Age at maturity (2)	-	-	-	-	-
Life span (0)	-	-	-	-	-
Length effects removed					
Length at maturity	0.52	.6046	6	94	.06
Length at birth	1.88	.1783	16	84	.16
Fecundity	13.19	.0012	33	67	.33
Gestation	0.01	.9093	.15	99.85	0
Age at maturity	-	-	-	-	-
Life span	-	-	-	-	-
Viviparous mode (189 species)					
Length effects included					
Length (189)	13.98	.0001	57	43	.57
Length at maturity (196)	7 [illegible]	.0001	54	46	.54
Length at birth (126)	1[illegible]	.0001	69	31	.69
Fecundity (123)	2.76	.0012	28	72	.28
Gestation (37)	10.04	.0001	67	33	.67
Age at maturity (23)	1.20	.1929	28	72	.28
Life span (20)	1.11	.3969	29	71	.29
Length effects removed					
Length at maturity	3.51	.0002	36	64	.36
Length at birth	4.68	.0001	41	59	.41
Fecundity	4.11	.0001	37	63	.37
Gestation	5.42	.0001	52	48	.52
Age at maturity	3.30	.0300	42	58	.42
Life span	1.32	.3109	32	68	.32

Table 17. Principal component analysis of life-history traits by mode of reproduction after phylogenetic (family) effects have been removed.

Analysis	% Variance exlained by			
Oviparous mode (2 families, 9 species)	PC1	PC2	PC3	Total
Length effects included				
9 species--family effects removed	66.09	23.49	10.13	99.71
Length effects removed				
9 species--length + family effects removed	61.06	30.40	8.54	100.00
Viviparous mode (8 families, 72 species)				
Length effects included				
72 species--family effects removed	71.43	23.85	0.03	98.61
Length effects removed				
72 species--length + family effects removed	61.42	27.72	10.86	100.00

Table 18. Unrotated component loadings for principal components 1 and 2 for each mode of reproduction.

Analysis	Length	Length at maturity	Birth length	Fecundity
OVIPAROUS MODE				
Principal component 1				
Length effects included				
9 species--family effects removed	.9274	.9743	.8419	-.3541
Length effects removed				
9 species--length + family effects removed		.9289	.7990	-.5748
Principal component 2				
Length effects included				
9 species--family effects removed	.2426	.1348	-.0328	.9282
Length effects removed				
9 species--length + family effects removed		.0472	.5203	.7994
VIVIPAROUS MODE				
Principal component 1				
Length effects included				
72 species--family effects removed	.9730	.9724	.8134	.5505
Lenth effects removed				
72 species--length + family effects removed		.6201	.9012	-.8036
Principal component 2				
Length effects included				
72 species--family effects included	.0412	-.0729	-.5240	.8198
Length effects removed				
72 species--length + family effects removed		.7669	-.0959	.4841

Table 19. Changes in correlation matrices derived for each mode of reproduction analysis after the removal of size and family effects.

Analysis	Length effects included			Analysis	Length effects removed	
	Length at maturity	Birth length	Fecundity		Birth length	Fecundity
A. Oviparous mode				C. Oviparous mode		
Length	.9749	.6252	-.1352	Length at maturity	.6560	-.4321
Length at maturity		.7280	-.2379	Birth length		-.0960
Birth length			-.2670			
B. Viviparous mode				D. Viviparous mode		
Length	.9376	.7301	.5474	Length at maturity	.4153	-.1844
Length at maturity		.7903	.4553	Birth length		-.6245
Birth length			.0576			

Table 20. Factorial analysis of variance on scores of PC1 and PC2 (dependent variables) and ecological variables with family effects removed.

Analysis	df	F	P	% Variance explained by Type 1 SS
Principal component 1				
Length effects included				
Habitat	2,66	0.62	.5416	2
Zone	2,66	2.81	.0679	7
Diet	2,66	6.58	.0026	16
Region	2,66	0.57	.5659	1
Length effects removed				
Habitat	2,66	0.03	.9705	0
Zone	2,66	0.76	.4706	2
Diet	2,66	2.35	.1038	7
Region	2,66	2.48	.0924	7
Principal component 2				
Length effects included				
Habitat	2,66	0.66	.5222	2
Zone	2,66	0.52	.5975	2
Diet	2,66	1.57	.2166	5
Region	2,66	1.71	.1894	5
Length effects removed				
Habitat	2,66	4.37	.0169	12
Zone	2,66	1.30	.2796	4
Diet	2,66	0.47	.6287	2
Region	2,66	0.16	.8533	0

Table 21. Mean values of traits used in analysis of ecological group: 11 families (223 species). Actual number of species used in parentheses. Blanks '–' indicate insufficient data. Mode of reproduction is coded as binary data.

Family	Length	Length at maturity	Length at birth	Fecundity	Gestation	Age at maturity	Life span	Mode[a]
Hexanchidae	271.3 (4)	225.8 (4)	46.7 (3)	38.9 (3)	–	–	–	1 (4)
Squalidae	91.1 (49)	69.0 (21)	24.9 (20)	24.9 (20)	20.3 (4)	–	–	1 (49)
Pristiophoridae	132.6 (4)	–	30.2 (3)	9.3 (2)	–	–	–	1 (4)
Heterodontidae	105.0 (6)	66.8 (3)	17.6 (5)	18.0 (3)	8.9 (4)	17.2 (2)	–	0 (6)
Lamnidae	427.6 (5)	–	90.5 (4)	6.7 (5)	–	5.8 (2)	18.4 (2)	1 (4)
Proscylliidae	50.0 (6)	26.8 (3)	12.3 (3)	2.0 (2)	–	–	–	0 (2) 1 (4)
Triakidae	119.8 (32)	83.8 (20)	28.3 (27)	9.3 (29)	10.9 (10)	4.0 (6)	15.5 (2)	1 (32)
Carcharhinidae	204.9 (40)	150.5 (34)	52.6 (39)	10.6 (35)	11.4 (18)	4.5 (13)	16.9 (13)	1 (40)
Sphyrnidae	225.4 (8)	181.5 (5)	43.0 (7)	21.2 (8)	7.5 (2)	–	–	1 (8)
Scyliorhinidae	57.0 (60)	48.4 (17)	12.0 (20)	4.2 (27)	8.7 (6)	–	–	0 (44) 1 (16)
Squatinidae	152.0 (9)	111.7 (3)	26.8 (4)	11.2 (3)	–	–	–	1 (9)

[a]Mode coded 0 = oviparous (52 species); 1 = viviparous (170 species).

Table 22. Summary of mode of reproduction and ecological categories associated with 11 families (223 species) of sharks Number of species used in parentheses.

	Mode		Habitat			Zone			Diet			Region		
Taxon	Oviparous	Viviparous	Benthic	Pelagic	Both	Ins.	Off.	Oceanic	Invert S. Fish	L. Fish	Omnivorous	North	South	Cosmopolitan
Hexanchidae (4)	0	4	3	0	1	1	1	2	2	1	1	0	3	1
Squalidae (49)	0	49	24	5	11	1	40	5	29	2	0	13	7	29
Pristiophoridae (4)	0	4	4	0	0	0	2	2	3	0	0	2	2	0
Heterodontidae (6)	6	0	6	0	0	2	1	3	5	0	0	2	2	2
Lamnidae (5)	0	5	0	2	0	0	0	5	3	0	2	1	0	4
Proscyllidae (6)	2	4	6	0	0	0	6	0	4	0	0	2	2	2
Triakidae (32)	0	32	29	2	-	10	7	12	25	0	0	8	12	9
Carcharhinidae (40)	0	40	9	22	2	20	3	17	26	0	8	3	0	37
Sphyrnidae (8)	0	8	0	5	0	4	0	3	6	0	0	1	1	5
Scyliorhinidae (60)	43	16	59	0	0	8	40	11	23	0	0	36	15	8
Squatinidae (9)	0	9	7	0	2	0	5	4		6		3	3	3

Table 23. Analyses of variance of each life-history trait among the categories of family, mode of reproduction, and ecological categories. Only families with 4 or more species are used.

Category	Sample size	Life history traits																					
		Length			Length at maturity			Birth length			Fecundity			Gestation			Age at maturity			Life span			
		df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	
Family	10	10,231	27.51	.0001	10,101	11.57	.0001	10,124	31.86	.0001	10,131	7.99	.0001	6,38	7.71	.0001	4,19	3.64	.0231	3,14	0.40	.7584	
Mode	2	1,221	37.56	.0001	1,110	23.29	.0001	1,133	63.71	.0001	1,140	26.49	.0001	1,43	9.29	.0039	1,22	7.27	.0132	0,19	-	-	
Diet	3	2,143	25.86	.0001	2,87	13.91	.0001	2,103	12.25	.0001	2,108	5.96	.0035	I,38	0.04	.8396	1,22	1.26	.2745	1,16	0.28	.6045	
Region	3	2,219	16.21	.0001	2,108	7.09	.0113	2,131	18.33	.0001	2,138	4.15	.0178	2,38	5.78	.0061	2,21	2.54	.1031	0,19	-	-	
Habitat	3	2,203	32.70	.0001	2,101	12.67	.0001	2,123	32.11	.0001	2,129	4.12	.0185	2,38	1.11	.3407	2,20	0.05	.9471	2,14	0.11	.8999	
Zone	3	2,218	33.04	.0001	2,108	10.30	.0001	2,131	15.45	.0001	2,138	6.66	.0017	2,41	5.78	.0062	1,22	8.58	.0078	1,16	2.14	.1629	

Table 24. Mean trait values of sharks associated with ecological categories and mode of reproduction for 223 species.

Trait	Habitat						Zone						Diet					
	Benthic		Pelagic		Both		Inshore		Offshore		Oceanic		Invertebrates and small fish		Large fish		Omnivores	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
Length	91.2	4.4	251.0	23.7	152.9	30.9	135.1	10.8	83.2	5.7	187.5	16.8	126.0	7.0	396.0	61.2	385.0	44.5
Length at maturity	78.9	4.4	166.2	15.2	138.4	53.4	109.1	10.3	73.2	9.1	129.1	12.9	97.7	6.9	200.0	-	241.6	27.9
Birth length	24.8	1.6	56.1	3.7	31.8	4.3	35.8	2.7	23.2	2.4	43.3	3.4	34.0	1.9	42.0	6.0	30.5	6.3
Fecundity	8.4	1.1	14.8	3.8	7.9	1.8	10.3	2.5	6.4	0.9	12.7	2.5	8.9	0.7	46.0	36.0	25.2	12.8
Gestation	11.2	0.9	11.2	0.6	14.7	3.2	9.9	0.8	16.3	2.5	10.8	0.6	11.6	0.7	-	-	6.6	0.7
Age at maturity	7.1	2.9	5.7	0.7	9.3	7.3	3.0	0.8	-	-	7.6	0.6	6.1	1.4	-	-	17.7	2.3
Life span	17.0	8.0	18.5	2.0	17.8	10.0	14.7	3.9	-	-	18.9	2.1	17.4	2.8	-	-		

(Cont'd.)

Trait	Region						Mode of reproduction			
	North		South		Cosmopolitan		Oviparous		Viviparous	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
Length	88.3	8.2	97.1	6.3	164.3	12.4	63.9	3.6	144.7	8.4
Length at maturity	72.0	9.3	78.1	8.2	128.1	10.5	49.7	3.9	118.2	7.3
Birth length	20.4	2.2	24.3	1.8	42.5	2.5	13.7	1.2	39.0	2.0
Fecundity	6.8	1.2	7.8	1.4	12.0	2.1	5.0	1.2	11.1	1.5
Gestation	10.2	0.6	8.0	1.4	12.4	0.8	8.8	0.9	11.9	0.7
Age at maturity	2.3	0.2	12.5	5.6	5.7	0.9	17.5	5.4	5.2	0.8
Life span	-	-	-	-	17.5	1.9	-	-	17.5	1.9

Table 25. Scheffe's multiple comparison of means test of life history traits associated with ecological categories and mode of reproduction. * = significant at the .05 level, N.S. = not significant, and I.D. = insufficient data.

Trait	Habitat level			Zone level			Diet level			Region level			Mode level
	1 vs 2	1 vs 3	2 vs 3	1 vs 2	1 vs 3	2 vs 3	1 vs 2	1 vs 3	2 vs 3	1 vs 2	1 vs 3	2 vs 3	1 vs 2
Length	*	*	*	*	*	*	*	*	N.S.	N.S.	*	*	*
Length at maturity	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Birth length	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	*	*	N.S.	*
Fecundity	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	*
Gestation	N.S.	N.S.	N.S.	*	N.S.	*	I.D.	I.D.	N.S.	N.S.	N.S.	*	*
Age at maturity	N.S.	N.S.	N.S.	I.D.	*	I.D.	I.D.	I.D.	N.S.	*	N.S.	N.S.	*
Life span	N.S.	N.S.	N.S.	I.D.	N.S.	I.D.	I.D.	I.D.	N.S.	I.D.	I.D.	I.D.	I.D.

Habitat level codes: (1) benthic, (2) pelagic, and (3) benthic/pelagic.
Zone level codes: (1) inshore, (2) offshore, and (3) oceanic.
Diet level codes: (1) invertebrates and small fish, (2) large fish, and (3) ominivores.
Region level codes: (1) north, (2) south, and (3) cosmopolitan.
Mode level codes: (1) oviparous and (2) viviparous.

Table 26. Bartlett's test of homogeneity of variances associated with mean length in various ecological categories.

Trait	Habitat	Zone	Diet	Region
Length	*	N.S.	*	*

Table 27. One-way ANOVA comparisons of standardized residual variation in life history traits among families, mode of reproduction, and ecological categories after removal of effects of size. I.D. = Insufficient Data.

Trait	Comparison	df	F	P
Length at maturity	Among families	10/101	1.76	.0767
	Among modes	1/110	0.00	.9777
	Among diets	2/87	0.00	.9967
	Among regions	2/108	2.11	.1266
	Among habitats	2/101	0.39	.6756
	Among zones	2/108	1.96	.1464
Birth length	Among families	10/124	6.43	.0001
	Among modes	1/133	30.68	.0001
	Among diets	2/103	2.74	.0690
	Among regions	2/131	10.17	.0001
	Among habitats	2/123	1.81	.1676
	Among zones	2/131	1.08	.3426
Fecundity	Among families	10/131	6.12	.0001
	Among modes	1/140	4.83	.0296
	Among diets	2/108	0.75	.4754
	Among regions	2/138	0.43	.6482
	Among habitats	2/129	0.38	.6825
	Among zones	2/138	0.39	.6756
Gestation	Among families	6/38	7.12	.0001
	Among modes	1/43	8.31	.0061
	Among diets	1/38	0.00	.9636
	Among regions	2/41	5.29	.0090
	Among habitats	2/38	1.03	.3669
	Among zones	2/41	6.06	.0050
Age at maturity	Among families	4/19	6.71	.0015
	Among modes	1/22	12.05	.0022
	Among diets	1/22	0.02	.8804
	Among regions	2/21	3.80	.0389
	Among habitats	2/20	0.36	.6995
	Among zones	1/22	5.35	.0305
Life span	Among families	3/14	1.27	.3233
	Among modes	i.d.	-	-
	Among diets	1/16	0.55	.4701
	Among regions	i.d.	-	-
	Among habitats	2/14	0.22	.8074
	Among zones	1/16	0.37	.5510

Table 28. One-way ANOVA comparisons of standardized residual variation in life history traits among mode of reproduction and ecological categories after removal of effects of size and family. I.D. = Insufficient Data.

Trait	Comparison	df	F	P
	Family-specific			
Length at maturity	Among modes	1/108	.00	.9917
	Among diets	2/85	0.85	.4299
	Among regions	2/106	1.91	.1532
	Among habitats	2/99	0.07	.9308
	Among zones	2/106	0.70	.4965
Birth length	Among modes	1/133	.04	.8397
	Among diets	2/103	1.66	.1952
	Among regions	2/131	4.75	.0102
	Among habitats	2/123	0.27	.7658
	Among zones	2/131	0.14	.8724
Fecundity	Among modes	I.D.	-	-
	Among diets	1/19	0.05	.8334
	Among regions	2/25	0.20	.8226
	Among habitats	2/24	0.09	.9128
	Among zones	2/25	1.70	.2035
Gestation	Among modes	1/40	0.22	.6430
	Among diets	1/36	0.78	.3826
	Among regions	2/39	1.72	.1922
	Among habitats	2/36	.24	.7888
	Among zones	2/39	6.55	.0035
Age at maturity	Among modes	I.D.	-	-
	Among diets	1/17	0.02	.8808
	Among regions	2/16	1.08	.3636
	Among habitats	2/15	0.94	.4111
	Among zones	1/17	0.73	.4035
Life span	Among modes	I.D.	-	-
	Among diets	1/11	0.08	.7768
	Among regions	I.D.	-	-
	Among habitats	2/9	2.04	.1854
	Among zones	1/11	0.09	.7737

Table 29. One-way ANOVA comparisons of standardized residual variation in life history traits among families after adjusting for the effects of ecology, mode of reproduction, and size. I.D. = Insufficient Data.

Trait	Comparisons among families	df	F	P
Length at maturity	Mode-specific	10/101	1.73	.0833
	Diet-specific	10/100	1.81	.0678
	Region-specific	10/100	1.72	.0853
	Habitat-specific	10/101	1.36	.2111
	Zone-specific	10/100	1.17	.3190
Birth length	Mode-specific	10/124	3.24	.0010
	Diet-specific	10/122	5.28	.0001
	Region-specific	10/123	5.27	.0001
	Habitat-specific	10/124	4.48	.0001
	Zone-specific	10/123	6.16	.0001
Fecundity	Mode-specific	10/131	5.66	.0001
	Diet-specific	10/129	5.31	.0001
	Region-specific	10/130	4.72	.0001
	Habitat-specific	10/131	3.85	.0001
	Zone-specific	10/130	5.17	.0001
Gestation	Mode-specific	6/38	4.21	.0024
	Diet-specific	6/38	7.58	.0004
	Region-specific	6/37	3.92	.0042
	Habitat-specific	6/38	4.37	.0019
	Zone-specific	6/37	5.52	.0004
Age at maturity	Mode-specific	I.D.	-	-
	Diet-specific	4/19	3.36	.0308
	Region-specific	4/16	3.54	.0300
	Habitat-specific	3/17	1.49	.2533
	Zone-specific	4/19	2.62	.0676
Life span	Mode-specific	I.D.	-	-
	Diet-specific	3/14	1.32	.3067
	Region-specific	3/14	1.27	.3233
	Habitat-specific	2/10	0.44	.6584
	Zone-specific	3/14	0.35	.7910

Class: Chondricthyes

Subclass: Elasmobranchii

Cohort: Euselachii ('modern' sharks)

	Galeormorphii	Batoidea	Squalormorphii	Squatinomorphii
Superorder				
	-Heterodontiformes (bull head sharks) 1 family, 1 Genus 8 species	skates rays sawfishes	-Hexanchiformes (cow sharks) 2 families, 4 Genera 5 species	-Squatiniformes (angel sharks) 1 family, 1 Genus 13 species
Order	-Orectolobiformes (blind, nurse, zebra, and whale sharks) 7 families, 13 Genera 31 species		-Squaliformes (dogfish sharks) 3 families, 18 Genera 73 species	
	-Carcharhiniformes (cat, hound, and hammerheads) 8 families, 48 Genera 193 species		-Pristiophoriformes (saw sharks) 1 family, 2 Genera 5 species	
	-Lamniformes (sand tiger, goblin, crocodile, thresher, mackerel, basking sharks) 7 families, 10 Genera 16 species			

Fig. 1. Interrelationships of living elasmobranchs according to the classification of Compagno (1973).

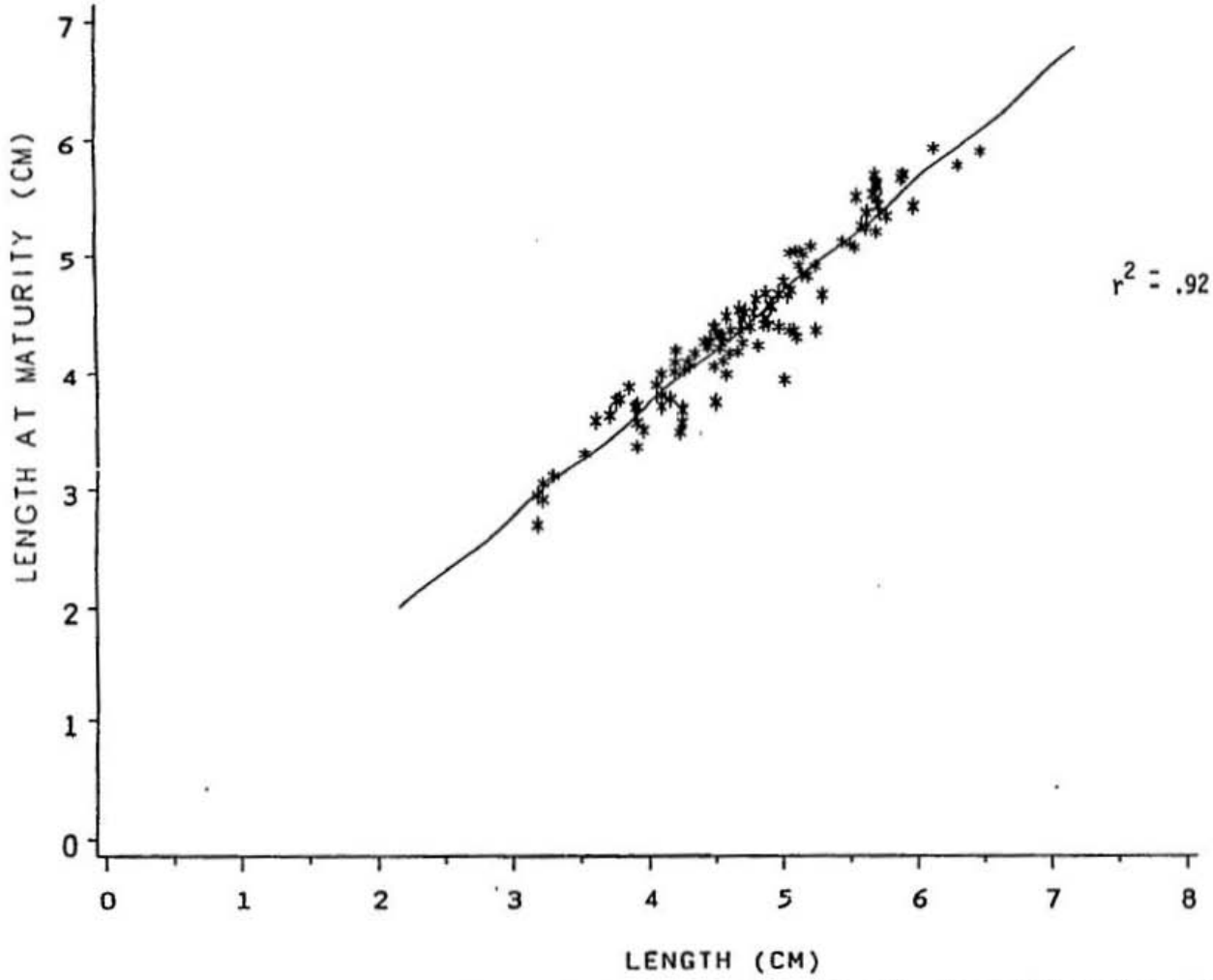

Fig. 2. Least squares regression of length at maturity against length in 109 species of sharks. Data are log-transformed.

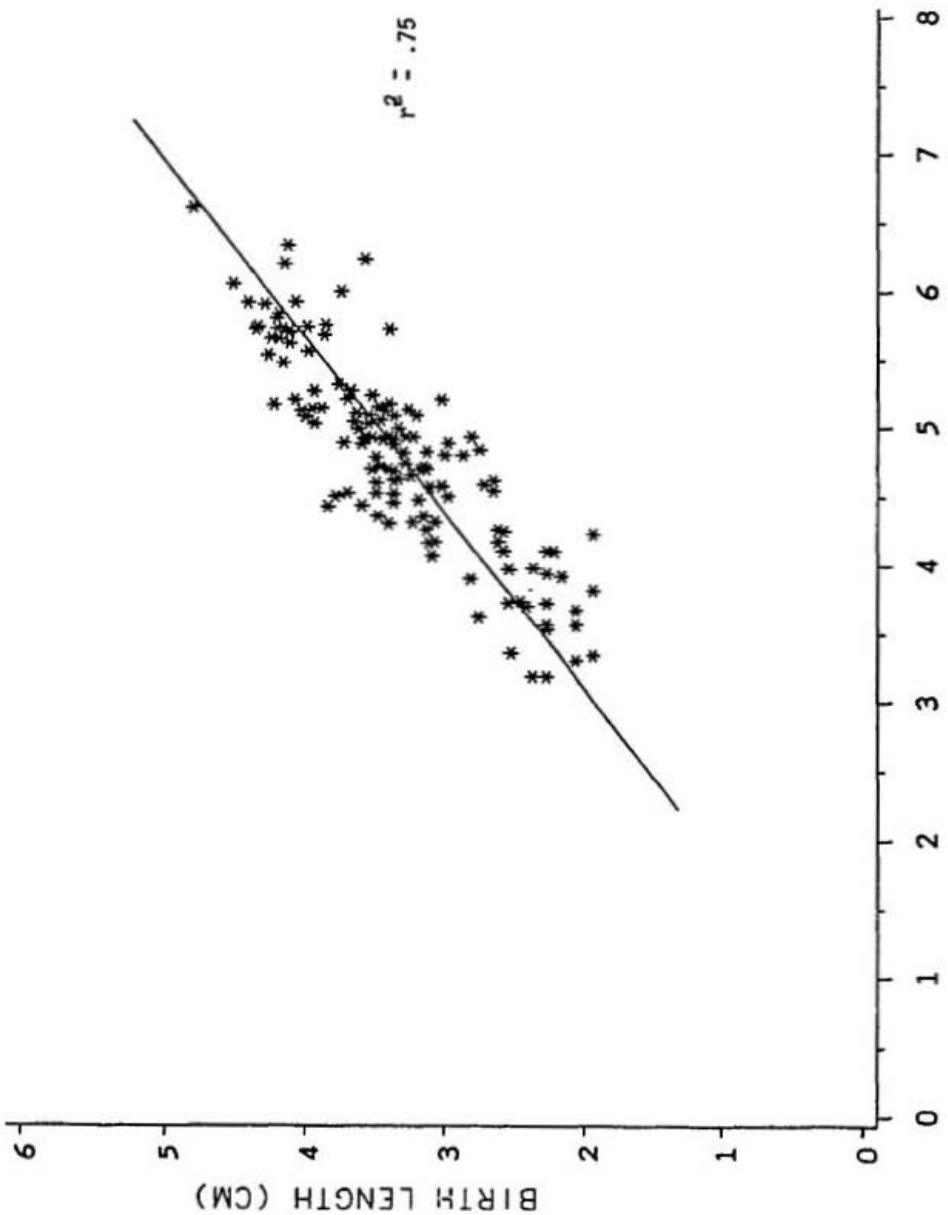

Fig.3. Least squares regression of birth length against length in 137 species of sharks. Data are log-transformed.

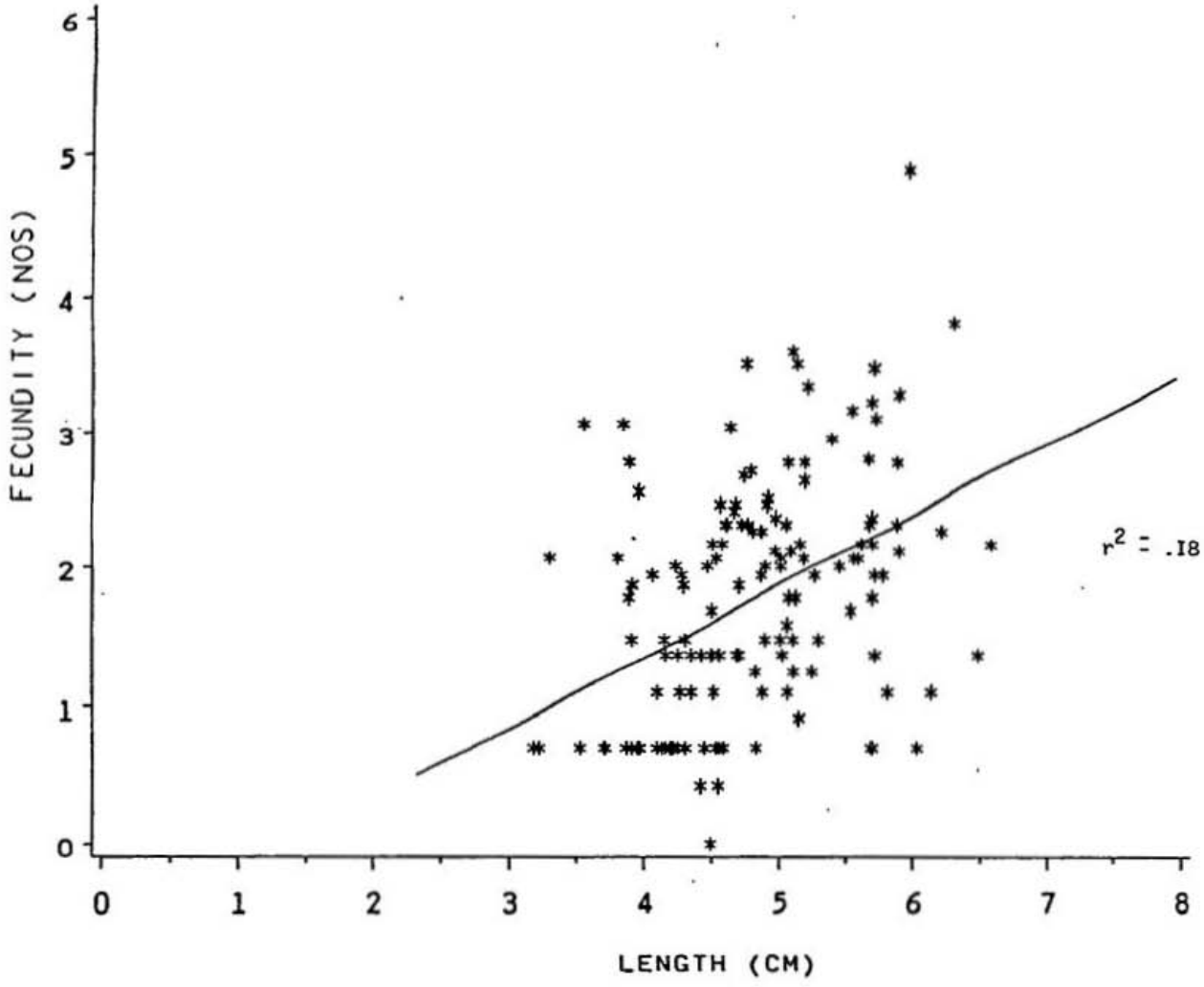

Fig.4. Least squares regression of fecundity against length in 144 species of sharks. Data are log-transformed.

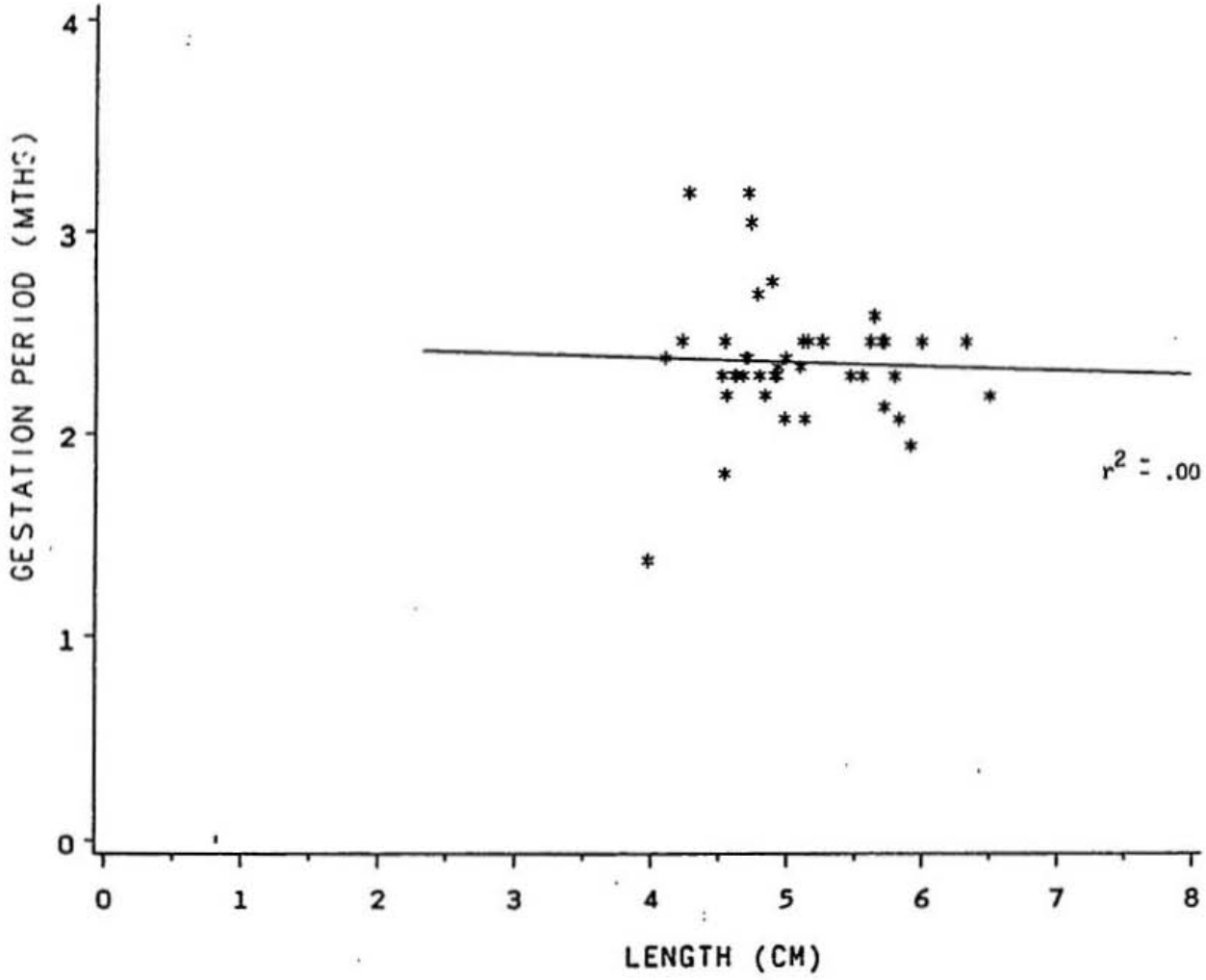

Fig. 5. Least squares regression of gestation period against length in 43 species of sharks. Data are log-transformed.

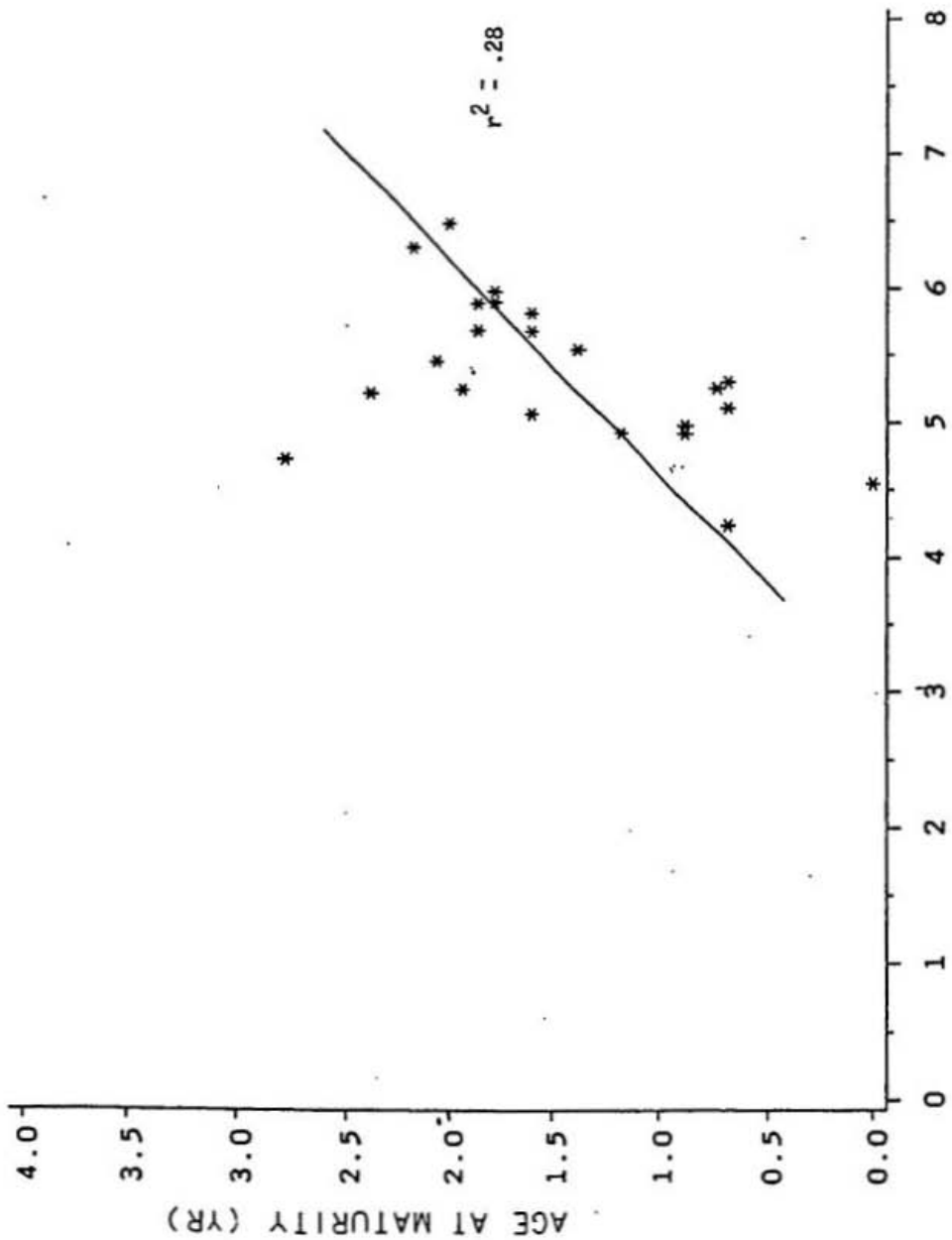

Fig. 6. Least squares regression of age at maturity against length in 23 species of sharks. Data are log-transformed.

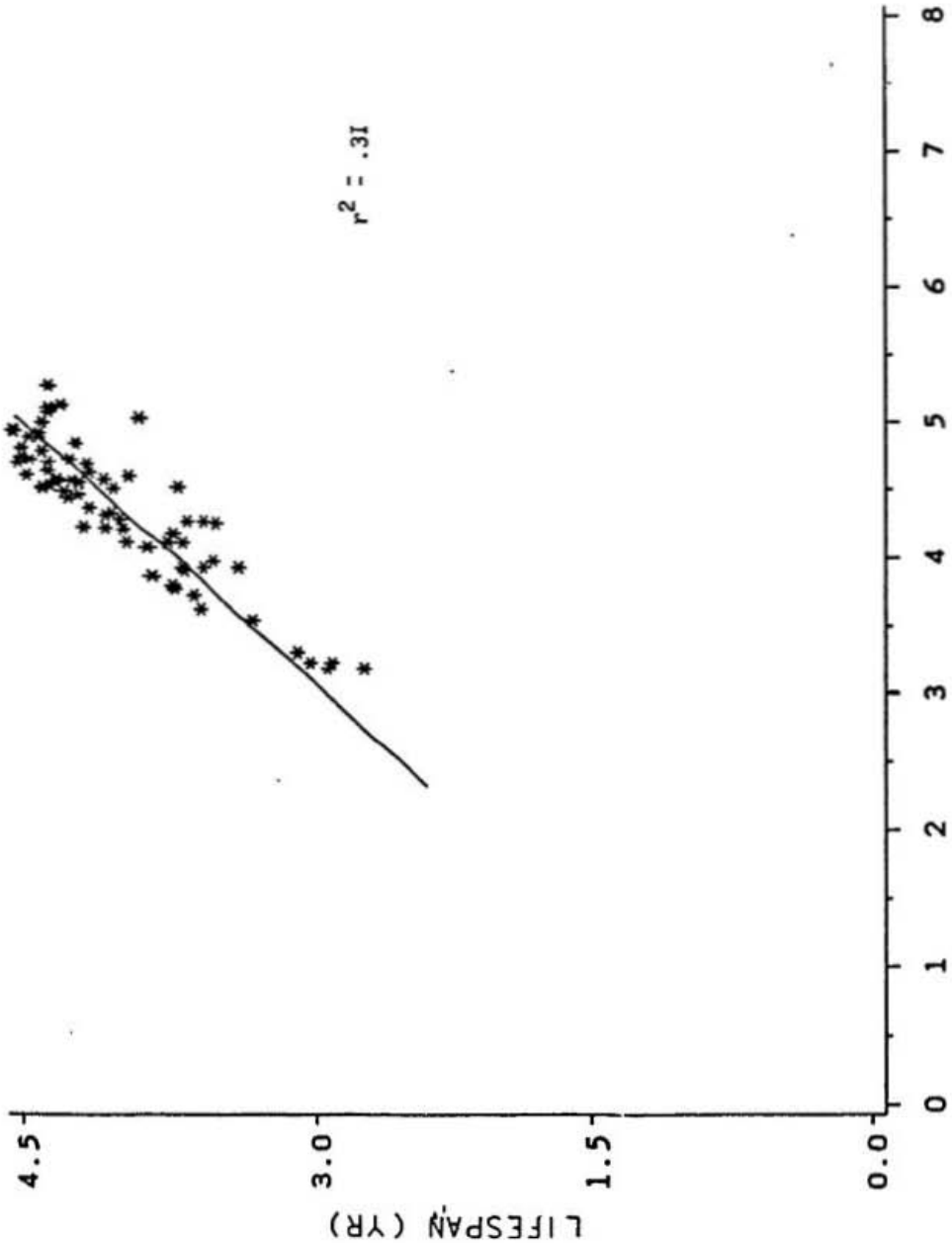

Fig.7. Least squares regression of life span against length in 20 species of sharks. Data are log_transformed.

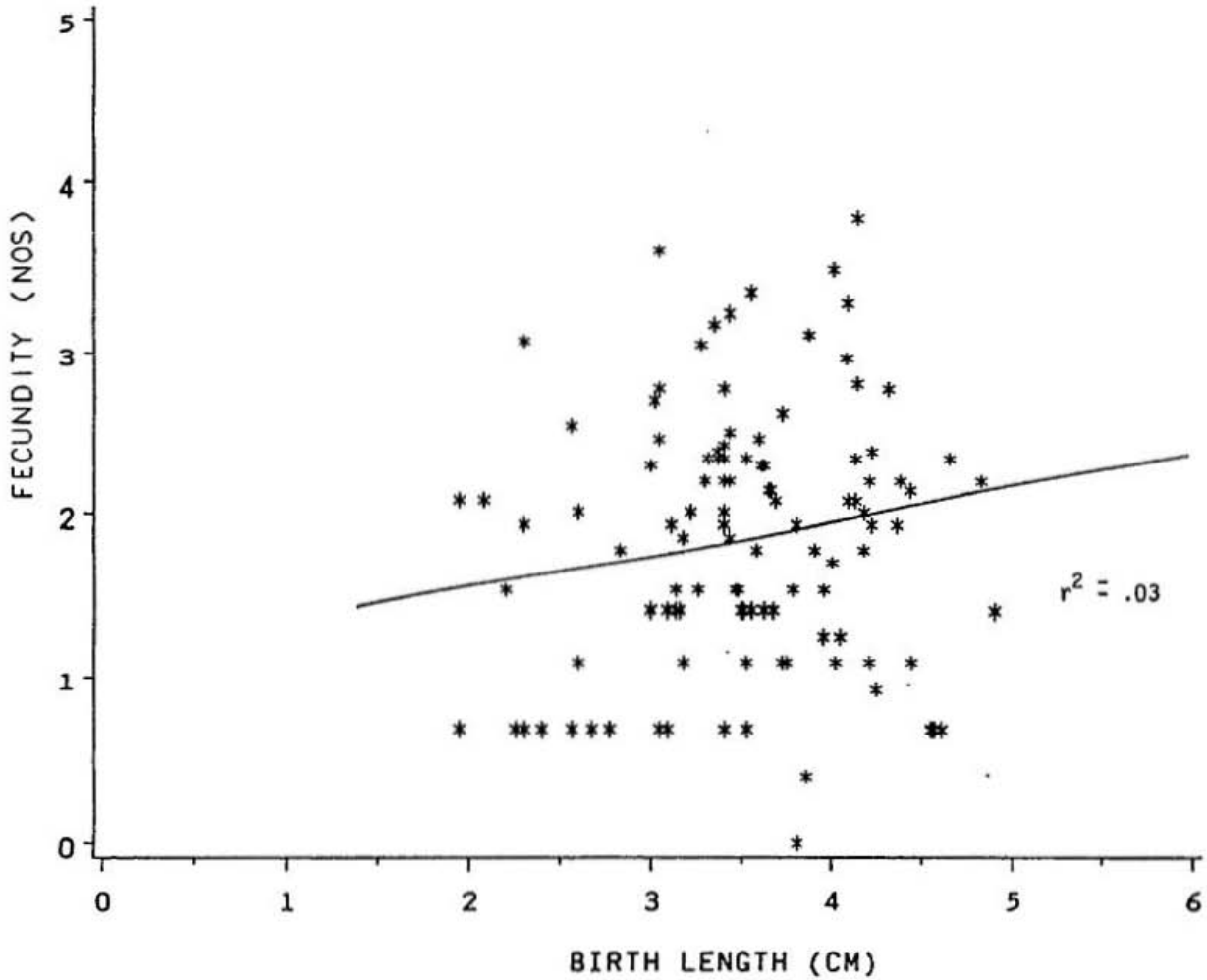

Fig.8. Least squares regression of fecundity against birth length in 144 species of sharks, with size effects included. Data are log-transformed.

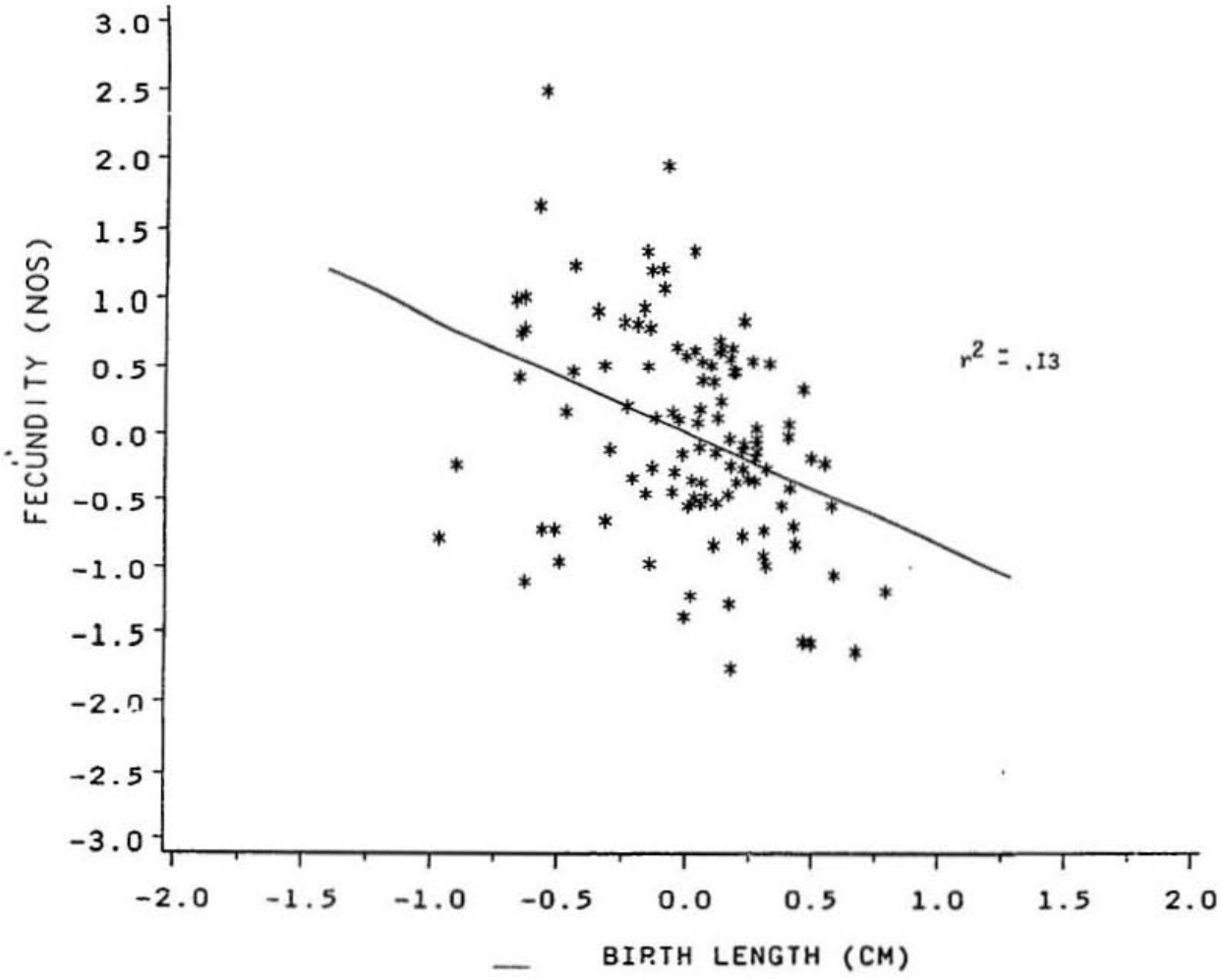

Fig.9. Least squares regression of fecundity against birth length in 144 species of sharks after size effects were removed in both traits. Data are log-transformed.

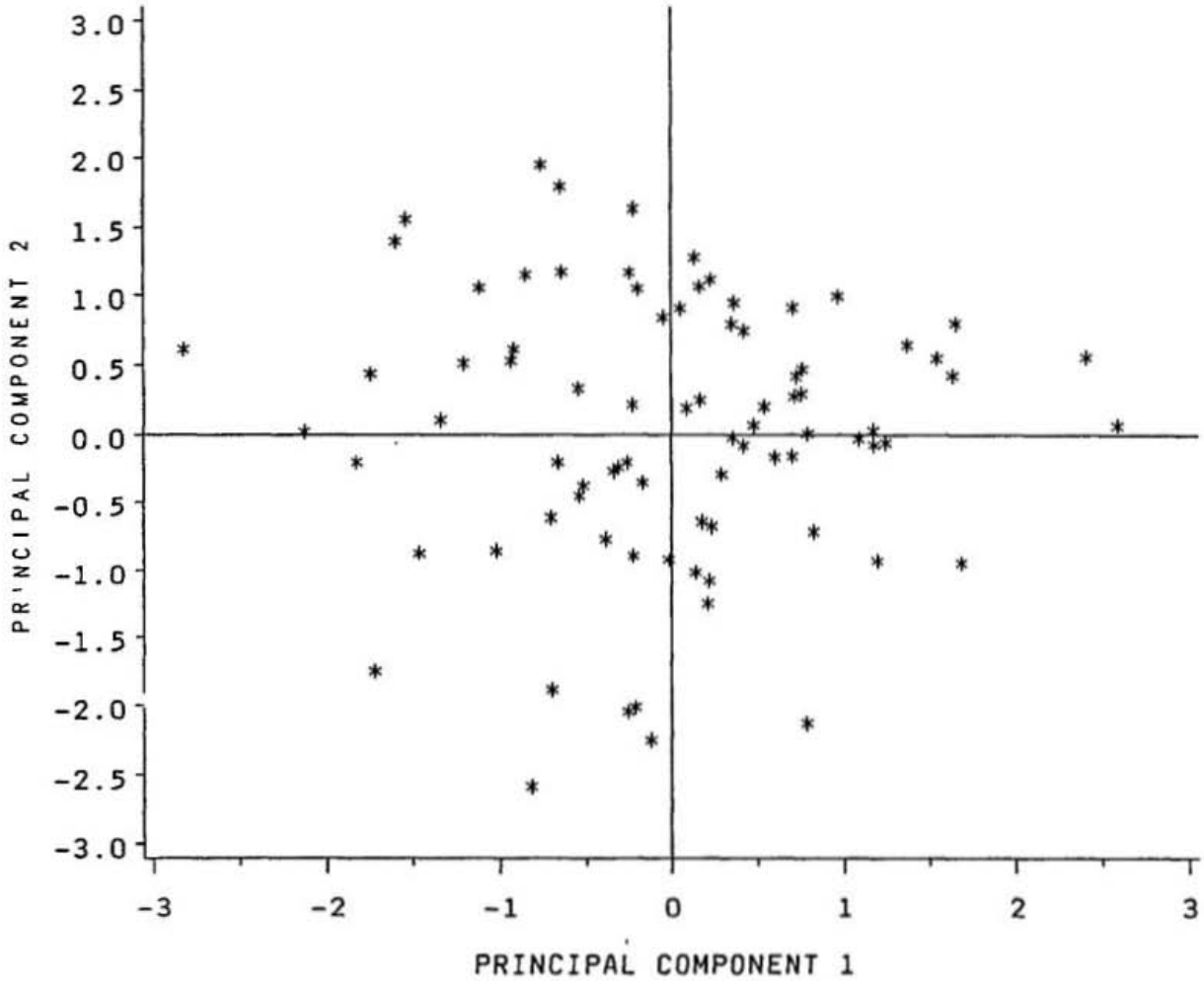

Fig.10. Scatter plot of principal component 2 scores against principal component I scores in 81 species. Size effects are included.

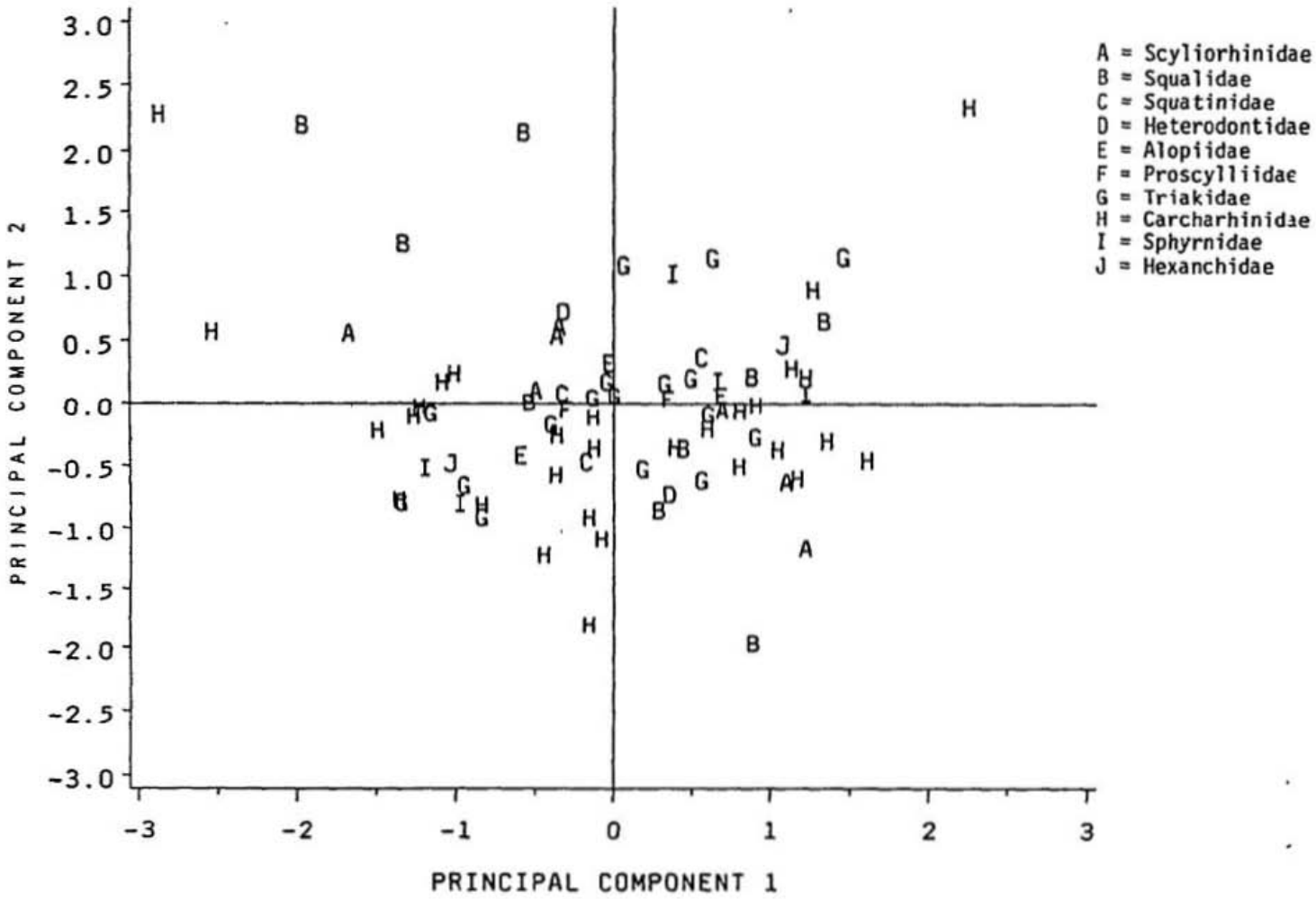

Fig.II. Scatter plot of principal component 2 scores against principal component I scores in 8I species. Family effects are removed.

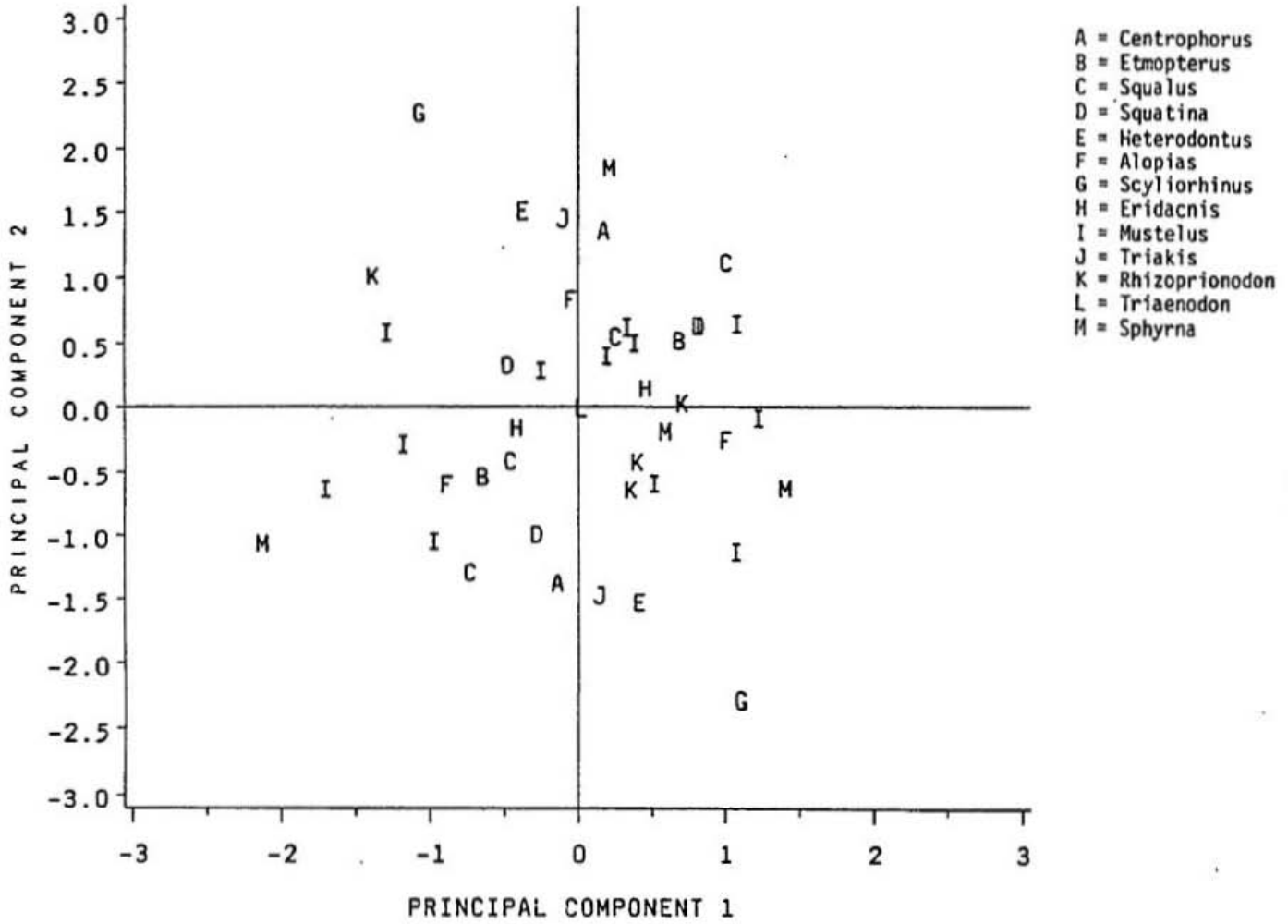

Fig. I2. Scatter plot of principal component 2 scores against principal component I scores in 63 species. Genus effects are removed.

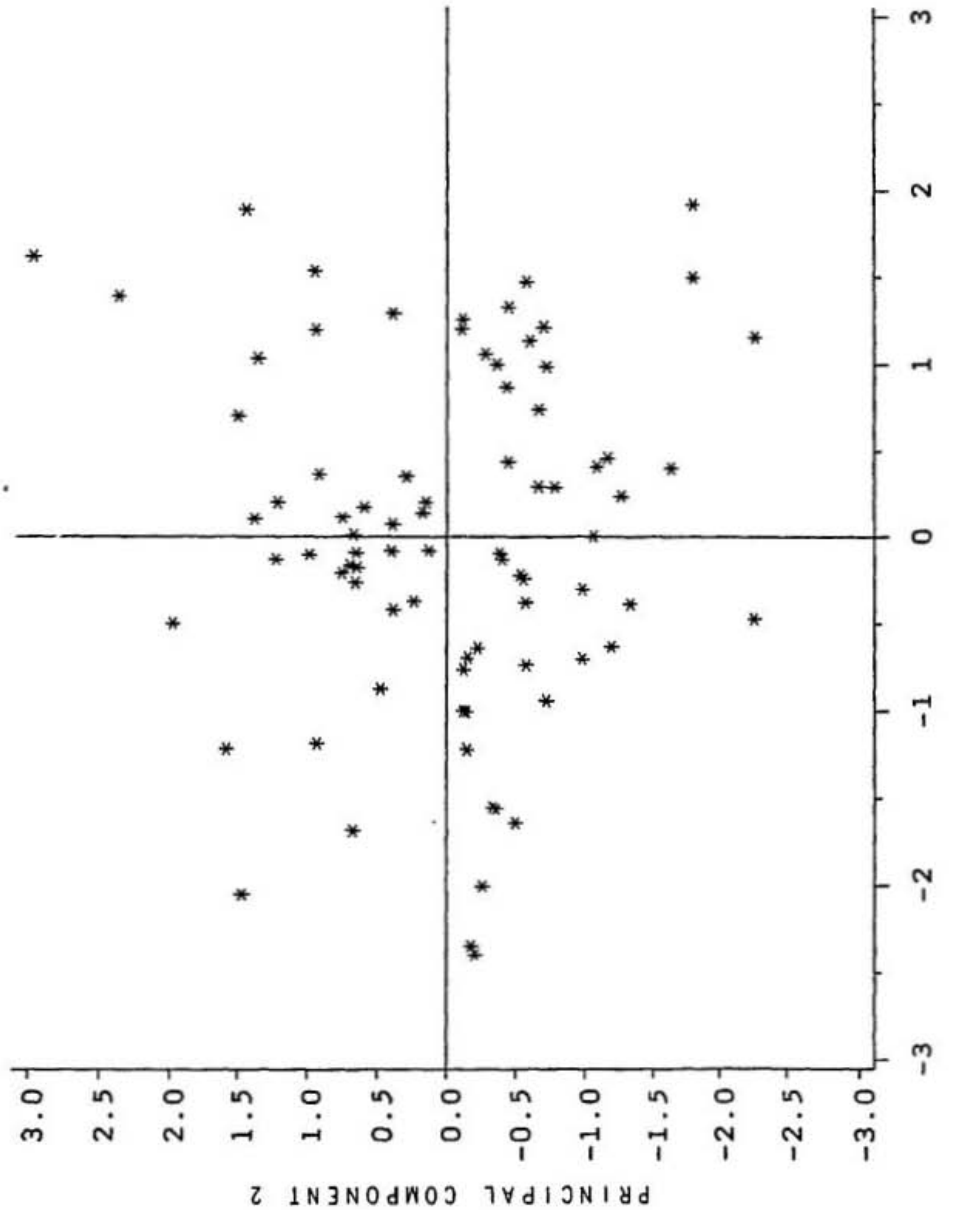

Fig. 13. Scatter plot of principal component 2 scores against principal component 1 scores in 81 species. Size effects are removed.

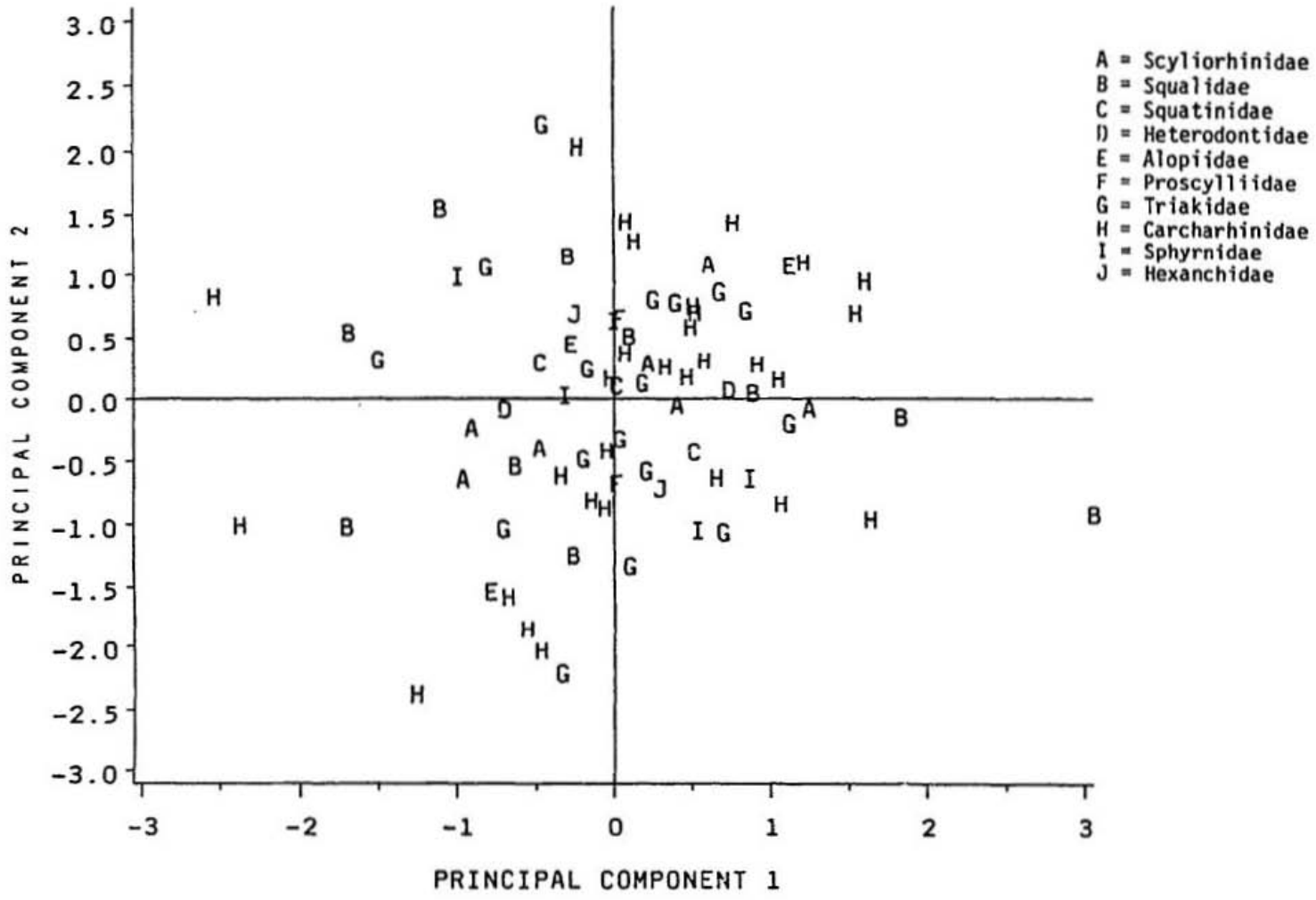

Fig I4. Scatter plot of principal component 2 scores against principal component I scores in 8I species. Size and family effects are removed.

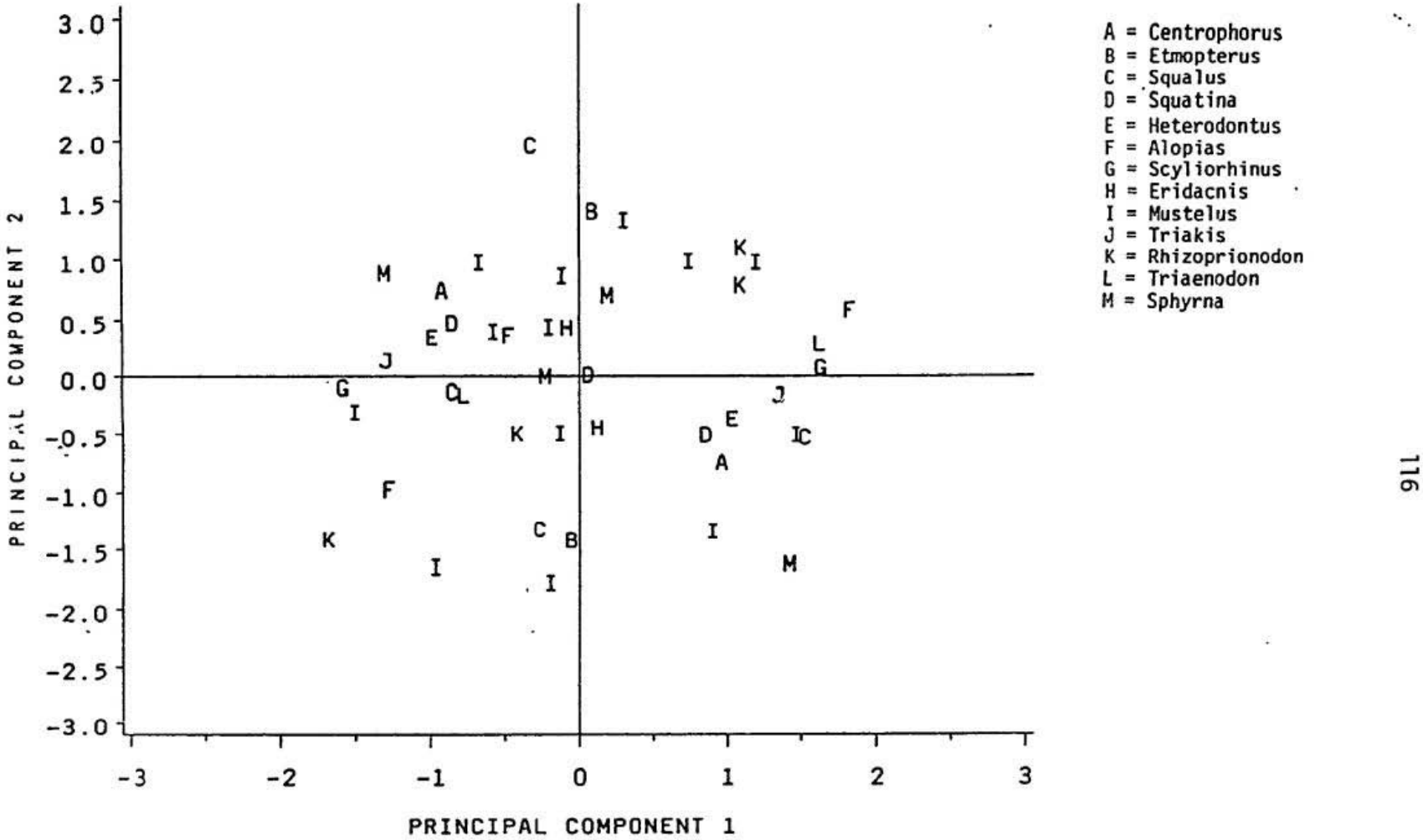

Fig. I5 Scatter plot of principal component 2 scores against principal component I scores in 63 species. Size and genus effects are removed.

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Order HEXANCHIFORMES													
Family HEXANCHIDAE													
Genus HEPTRANCHIAS													
H. perlo	137	93	20	26	-	-	-	1	2	1	2	3	A
Genus HEXANCHUS													
H. griseus	482	450	-	65	-	-	-	1	3	3	4	3	A,13
H. vitulus	178	160	13	-	-	-	-	1	3	1	2	2	A
Genus NOTORYNCHUS													
N. cepedianus	288	200	82	49	-	-	-	1	1	1	3	3	A,13
Order SQUALIFORMES													
Family ECHINORHINIDAE													
Genus ECHINORHINUS													
E. brucus	221.5	-	19.5	59.5	-	-	-	1	3	1	2	3	A
E. cookei	276.5	-	-	45.0	-	-	-	1	3	1	2	3	A
Family SQUALIDAE													
Genus ACULEOLA													
A. nigra	60	53	3	13.5	-	-	-	1	2	1	-	2	A
Genus CENTROPHORUS													
C. granulosus	150	-	-	36	-	-	-	1	2	3	2	3	A
C. harrissoni	116	-	-	-	-	-	-	1	2	-	-	2	A
C. lusitanicus	160	-	6	36	-	-	-	1	2	1	2	3	A
C. moluccensis	98	89	2	34	-	-	-	1	2	1	2	3	A
C. niaukang	159	-	-	-	-	-	-	1	2	-	-	1	A
C. squamosus	158	147.5	5	-	-	-	-	1	2	3	-	3	A
C. uyato	89	82	1	45	-	-	-	1	2	3	2	3	A
Genus CENTROSCYLLIUM													
C. fabriccii	64	-	-	14	-	-	-	1	2	1	2	3	A
C. kamoharai	44	43	-	-	-	-	-	1	2	1	2	1	A
C. nigrum	50	-	-	-	-	-	-	1	2	1	-	3	A
C. ritteri	43	42.5	-	-	-	-	-	1	2	1	2	1	A
Genus CENTROSCYMNUS													
C. coelolepis	114	-	14.5	-	-	-	-	1	2	1	2	3	A
C. crepidater	90	82	4.0	-	-	-	-	1	2	1	2	3	A
C. cryptacanthus	103	-	-	-	-	-	-	1	2	1	-	3	A
C. plunketi	170	149.5	3.0	-	-	-	-	1	2	1	2	2	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Genus CIRRHIGALEUS													
C. barbifer	122	100	10	–	–	–	–	1	2	1	–	3	A
Genus DALATIAS													
D. licha	159	–	16	30	–	–	–	1	2	3	2	3	A
Genus DEANIA													
D. calcea	90.5	-	9	30	–	–	–	1	2	3	2	3	A
D. histricosa	107.5	–	12	–	–	–	–	1	2	1	–	1	A
D. profundorum	73	93	6.5	31	–	–	–	1	2	1	2	3	A
D. quadrispinosum	110	–	–	–	–	–	–	1	2	–	2	2	A
Genus ETMOPTERUS													
E. bareri	75	–	–	–	–	–	–	1	2	1	–	2	A
E. hillianus	50	30	4.5	9	–	–	–	1	2	1	–	1	A
E. lucifer	34	–	–	–	–	–	–	1	2	1	2	3	A
E. polli	24	–	–	–	–	–	–	1	2	1	–	3	A
E. pusillus	42.5	–	–	–	–	–	–	1	2	3	2	3	A
E. schultzi	29	–	–	–	–	–	–	1	2	1	–	1	A
E. spinax	52.5	34.5	13	13	–	–	–	1	2	3	2	3	A
E. unicolor	53	–	–	–	–	–	–	1	–	–	–	1	A
E. virens	23	–	–	–	–	–	–	1	2	2	2	1	A
Genus EUPROTOMICRUS													
E. bispinatus	27	22.5	8	8	–	–	–	1	2	2	2	3	A
Genus HETEROSCYMNOIDES													
H. marleyi	28.5	–	–	12.8	–	–	–	1	2	3	–	2	A
Genus ISISTIUS													
I. brasiliensis	50	41	6.5	–	–	–	–	1	3	2	2	3	A
I. plutodus	42	–	–	–	–	–	–	1	2	2	2	1	A
Genus SCYMNODON													
S. obscurus	59	–	–	–	–	–	–	1	2	3	2	3	A
S. squamulosus	69	–	–	–	–	–	–	1	2	–	–	1	A
Genus SQUALIOLUS													
S. laticaudus	25	18.5	–	–	–	–	–	1	3	2	2	3	A
Genus SQUALUS													
S. acanthias	112.5	91.5	10.5	27.5	21	16.5	27.5	1	3	3	2	3	A,4,5,6,7,14
S. asper	103.5	–	21.5	26.5	–	–	–	1	1	1	2	3	A
S. blainvillei	95	60	4	23	–	–	–	1	3	1	2	3	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
S. japonicus	93	76.5	8	-	12	-	-	1	3	1	-	1	A
S. megalops	71	55	3	-	24	-	-	1	2	1	2	3	A
S. melanurus	75	-	-	-	-	-	-	1	3	-	2	2	A
S. mitsukurii	110	72	6.5	24	24	-	-	1	2	1	2	3	A
S. rancureli	77	65	3.0	24	-	-	-	1	2	1	-	2	A
Family OXYNOTIDAE													
Genus OXYNOTUS													
O. bruniensis	72	-	7	10	-	-	-	1	2	1	-	2	A
O. centrina	150	50	7.5	-	-	-	-	1	2	3	2	1	A
O. paradoxus	118	-	-	25	-	-	-	1	2	1	-	1	A
Order PRISTIOPHORIFORMES													
Family PRISTIOPHORIDAE													
Genus PLIOTREMA													
P. warreni	136	110	6.5	3..0	-	-	-	1	2	1	2	2	A
Genus PRISTIOPHORUS													
P. cirratus	137	-	-	27.5	-	-	-	1	3	1	2	1	A
P. japonicus	136	-	12	-	-	-	-	1	3	1	2	1	A
P. nudipinnis	122	-	-	28	-	-	-	1	2	1	-	2	A
Order SQUATINIFORMES													
Family SQUATINIDAE													
Genus SQUATINA													
S. aculeata	188	-	-	-	-	-	-	1	2	3	2	3	A
S. africana	108	91.5	9	31	-	-	-	1	3	1	2	2	A
S. argentina	170	-	-	-	-	-	-	1	2	1	-	2	A
S. australis	152	-	-	-	-	-	-	1	2	1	-	2	A
S. californica	108	97	10	23.5	-	-	-	1	3	1	2	3	A,8,10,11
S. dumeril	152	-	-	-	-	-	-	1	3	1	2	1	A
S. nebulosa	163	-	-	-	-	-	-	1	2	1	-	1	A
S. oculata	160	-	-	25.5	-	-	-	1	2	3	2	3	A
S. squatina	167	146.5	14.5	27.0	-	-	-	1	3	1	2	1	A
Order HETERODONTIFORMES													
Family HETERODONTIDAE													
Genus HETERODONTUS													
H. francisci	97	58	23	15.5	8	-	-	0	3	1	2	1	A
H. galeatus	137	-	-	17	5	11.8	-	0	3	1	2	2	A
H. japonicus	120	-	18	18	12	-	-	0	1	1	2	1	A
H. mexicanus	70	55	-	14	-	-	-	0	1	1	-	3	A
H. portusjacksoni	123	87.5	13	23.5	10.5	22.5	-	0	3	1	2	2	A
H. romalheira	83	-	-	-	-	-	-	0	2	1	2	3	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Order ORECTOLOBIFORMES													
Family PARASCYLLIDAE													
Genus CIRROSCYLLIUM													
C. formosanum	39	-	-	-	-	-	-	1	2	1	-	1	A
C. japonicum	49	-	-	-	-	-	-	1	-	-	-	1	A
Genus PARASCYLLIUM													
P. collare	86	-	-	-	-	-	-	0	2	1	-	2	A
P. ferrugineum	75	-	-	17	-	-	-	1	2	1	-	2	A
Family ORECTOLOBIDAE													
Genus ORECTOLOBUS													
O. maculatus	165	-	37	21	-	-	-	1	1	1	2	3	A
O. ornatus	288	-	-	20	-	-	-	1	1	1	-	3	A
Genus SUTORECTUS													
S. tentaculatus	92	-	-	-	-	-	-	1	-	-	-	2	A
Family HEMISCYLLIIDAE													
Genus CHILOSCYLLIUM													
C. griseum	74	-	-	-	-	-	-	0	1	1	2	3	A
C. indicum	65	-	-	-	-	-	-	0	1	1	-	3	A
C. plogiosum	95	-	-	-	-	-	-	0	1	1	-	3	A
C. punctatum	104	-	-	-	-	-	-	0	1	1	-	3	A
Genus HEMISCYLLIUM													
H. ocellatum	107	-	-	-	-	-	-	0	1	1	-	2	A
Family GINGLYMOSTOMATIDAE													
Genus GINGLYMOSTOMA													
G. cirratum	259	235	24.5	28.5	-	-	25	1	1	1	2	3	A
Genus NEBRIUS													
N. ferrugineus	260	-	8	40	-	-	-	1	1	1	2	3	A
Order LAMNIFORMES													
Family ODONTASPIDIDAE													
Genus EUGOMPHODUS													
E. taurus	300	260	2	100	8.5	-	-	1	3	3	2	3	A
Genus ODONTASPIS													
O. ferox	360	-	10.5	105	-	-	-	1	2	1	2	3	A
O. noronhai	326	-	-	-	-	-	-	1	2	1	-	3	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Family ALOPIIDAE													
Genus ALOPIAS													
A. pelagicus	297	277	2	96	-	-	-	1	3	2	-	3	A
A. superciliosus	461	355	3	85	-	-	-	1	3	2	2	3	A
A. vulpinus	654.5	343.5	4	134.5	9	7.5	50	1	3	2	4	3	A,11
Family LAMNIDAE													
Genus CARCHARODON													
C. carcharias	720	-	9	125	-	-	-	1	3	2	4	3	A,9,11
Genus ISURUS													
I. oxyrinchus	361	269	16	75	-	6.5	11.8	1	3	2	4	3	A
I. paucus	417	-	2	99.5	-	-	-	1	3	2	2	3	A
Genus LAMNA													
L. ditopis	305	-	4	-	-	-	-	1	3	2	2	1	A
L. nasus	305	-	3	67.5	8	5	25	1	3	2	2	3	A
Order CARCHARINIFORMES													
Family PROSCYLLIIDAE													
Genus CTENACIS													
C. fehlmanni	46	-	-	-	-	-	-	1	2	1	-	1	A
Genus ERIDACNIS													
E. barbouri	34	28	2	10	-	-	-	1	2	1	2	1	A
E. radcliffei	24	15.5	2	11	-	-	-	1	2	1	2	3	A
E. sinuans	37	37	-	16	-	-	-	0	2	1	2	2	A
Genus GOLLUM													
G. attenuatus	101	-	-	-	-	-	-	1	2	1	-	2	A
Genus PROSCYLLIUM													
P. habereri	58	-	-	-	-	-	-	0	2	1	2	3	A
Family TRIAKIDAE													
Genus FURGALEUS													
F. macki	131	-	10	20	-	-	-	1	2	1	2	2	A
Genus GALEORHINUS													
G. galeus	184.5	157.5	29	35	-	11	22	1	3	2	2	3	A
Genus GOGOLIA													
G. filewoodi	74	-	2	22	-	-	-	1	2	1	-	2	A
Genus HEMITRIAKIS													
H. japanica	120	91.5	15	20.5	10	-	-	1	3	1	2	3	A
H. leucoperiptera	96	-	12	21	-	-	-	1	1	1	-	1	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Genus HYPOGALEUS													
H. hyugaensis	118	–	10.5	34	15	–	–	1	2	1	2	3	A
Genus IAGO													
I. garricki	63.5	–	4.5	23	–	–	–	1	2	1	2	2	A
I. omanensis	49	–	6	17	–	–	–	1	2	1	2	1	A
Genus MUSTELUS													
M. antarcticus	157	80	10.5	–	–	–	–	1	3	1	2	2	A
M. asterias	145	82.5	11	29	11	2.4	–	1	3	1	2	1	A
M. californicus	124	70	3.5	–	–	–	–	1	3	1	2	1	A
M. canis	136	95	12	36.5	10	2.4	–	1	3	2	2	3	A
M. dorsalis	64	43	4	22	–	–	–	1	1	1	2	3	A
M. griseus	101	80	10.5	29	10	–	–	1	1	1	–	1	A
M. henlei	89	57	4	20	–	–	–	1	1	1	2	3	A
M. higmani	58	48	7	22.5	–	–	–	1	3	1	2	3	A
M. lenticulatus	137	96	12.5	31	10.5	3.3	–	1	3	1	2	2	A
M. lunulatus	170	–	–	33.5	–	–	–	1	3	1	–	1	A
M. manazo	106.4	66	11.5	30	10	2.5	9	1	1	1	2	3	A
M. mento	130	88	7	30	–	–	–	1	3	1	–	2	A
M. mosis	150	–	8	–	–	–	–	1	3	1	2	3	A
M. mustelus	162	80	8.5	39	10.5	–	–	1	3	1	2	3	A
M. norrisi	100	65	10.5	30	–	–	–	1	3	1	2	3	A
M. palumbes	90	–	5.5	–	–	–	–	1	3	1	2	2	A
M. punctulatus	191	80	–	40.5	12	2.1	–	1	1	1	2	1	A
M. schmitti	74	57.5	4.5	26	–	–	–	1	2	1	2	2	A,14
M. whitney	87	74	7.5	25	–	–	–	1	3	1	2	3	A
Genus SCYLLIOGALEUS													
S. quecketti	91	–	3	34	10	–	–	1	1	1	2	2	A
Genus TRIAKIS													
T. acutipinna	102	–	–	–	–	–	–	1	2	–	–	2	A
T. maculata	180	–	14	41.5	–	–	–	1	1	1	–	2	A
T. megalopterus	174	145	9	31	–	–	–	1	1	1	2	2	A
T. semifasciata	180	119.5	16	21	–	–	–	1	1	1	2	1	A,11
Family HEMIGALEIDAE													
Genus Hemigaleus													
H. microstoma	97.2	52.5	9	27	–	–	–	1	1	1	2	3	A
Genus HEMIPRISTIS													
H. elongatus	194	–	7	45	–	–	–	1	3	–	2	3	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Genus PARAGALEUS													
P. pectoralis	117	82.5	-	47	-	-	-	1	3	-	2	3	A
Family CARCHARINIDAE													
Genus CARCHARHINUS													
C. acronotus	200	103	4.5	44	-	2	-	1	1	2	2	3	A
C. albimarginatus	300	179.5	6	65.5	12	-	-	1	3	2	2	3	A
C. altimus	300	254	9	80	-	-	-	1	2	1	2	3	A
C. amblyrhynchoides	167	-	-	53.5	-	-	-	1	3	2	-	3	A
C. amblyrhynchos	190	129.5	3.5	52.5	12	7	25	1	3	2	2	3	A,2
C. amboinensis	280	210.5	-	71.5	-	-	-	1	1	1	2	3	A
C. brachyurus	292	240	16.5	63	-	5	12	1	3	2	2	3	A
C. brevipinna	278	185	9	67.5	13.5	-	-	1	3	2	4	3	A
C. cautus	135	-	-	37	-	-	-	1	1	-	2	2	A
C. dussumieri	83	72.5	4	37.5	-	-	-	1	1	-	-	3	A
C. falciformis	305	221.5	7	78.5	-	-	-	1	3	2	2	3	A,12
C. galapagensis	300	235	11	68.5	-	-	-	1	3	2	2	3	A
C. isodon	165	150	3.5	57.5	-	-	-	1	1	2	2	3	A
C. leucas	324	205	7	68.5	10	-	16	1	1	2	4	3	A
C. limbatus	255	155	5.5	55	10	4	12	1	3	2	4	3	A,12
C. longimanus	270	190	8	62.5	12	-	-	1	2	2	4	3	A
C. macloti	82.5	-	1.5	47.5	-	-	-	1	1	-	-	3	A
C. melanopterus	131	104	3	42.5	16	-	-	1	1	2	2	3	A
C. obscurus	365	278.5	8.5	84.5	-	6	18	1	3	2	4	3	A
C. perezi	247	160	-	73	-	-	-	1	1	1	2	3	A
C. plumbeus	234	163.5	7.5	65.5	10	8	30	1	3	2	4	3	A,1
C. porosus	134	84	4.5	32.5	10	-	-	1	1	1	2	3	A
C. sealei	94	71.5	1.5	-	9	1	5	1	1	-	2	3	A
C. signatus	178.5	-	8	60	-	-	-	1	2	2	2	3	A
C. sorrah	150	114	4.5	52.5	-	-	-	1	1	-	2	3	A
C. wheeleri	172	120	2.5	70	12	-	-	1	3	-	2	3	A
Genus GALEOCERDO													
G. cuvier	550	300	46	63.5	12	9	16	1	3	2	4	3	A,3,12
Genus ISOGOMPHODON													
I. oxyrhynchus	152	-	4	39.5	-	-	-	1	1	2	2	3	A
Genus LAMIOPSIS													
L. temminckii	168	130	6	50	8	-	-	1	1	-	-	1	A
Genus LAXODON													
L. macrorhinus	807	91	3	41.5	-	-	-	1	1	2	2	3	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Genus NEGAPRION													
N. brevirostris	295	239	10.5	62.5	12	6.5	27	1	1	2	4	3	A
Genus PRIONACE													
P. glauca	395.5	220	135	43.5	12	6	20	1	3	2	4	3	A
Genus RHIZOPRIONODON													
R. acutus	165	75.5	4.5	32	12	8	2	1	3	3	2	3	A
R. lanlandii	77	–	4.0	33.5	–	–	–	1	1	1	2	3	A
R. logurio	154	103	–	33	–	–	–	1	1	1	–	3	A
R. terraenovae	110	87.5	4.0	33	11	–	–	1	3	3	2	1	A,12
R. oligolinx	70	36.5	4	23.5	–	–	–	1	3	1	–	1	A
R. porosus	108	80	4	35	11	–	–	1	3	1	2	3	A
Genus [illegible]OLIODON													
S. laticaudus	69	34	7.5	13.5	–	2	6	1	1	2	2	3	A
Genus TRIAENODON													
T. obesus	158	107	3	56	–	5	25	1	1	1	2	3	A
Family SPHYRNIDAE													
Genus EUSPHYRA													
E. blochii	144	104	8.5	38.5	8	–	–	1	–	–	–	–	A
Genus SPHYRNA													
S. couardi	300	232.5	26	31	–	–	–	1	1	2	2	3	A
S. lewini	309	212	23	48.5	–	–	–	1	3	2	2	3	A
S. media	116.5	–	34	–	–	–	–	1	1	–	–	3	A
S. mokarran	366.5	275	27.5	60	7	–	–	1	3	2	2	3	A
S. tiburo	130	84	10	37.5	–	–	–	1	1	2	2	3	A
S. tudes	134	–	7.5	30	–	–	–	1	1	–	2	2	A
S. zygaena	304	–	33	55.5	–	–	–	1	3	2	2	3	A
Family SCYLIORHINIDAE													
Genus APRISTURUS													
A. atlanticus	25	–	–	–	–	–	–	1	2	1	–	1	A
A. brunneus	68	–	2	7	12	–	–	0	2	1	2	1	A
A. canutus	43	–	–	–	–	–	–	1	2	1	–	1	A
A. japonicus	63	–	–	–	–	–	–	0	2	1	–	1	A
A. kampae	52	–	2	–	–	–	–	0	2	1	–	1	A
A. laurussoni	67	–	–	–	–	–	–	1	2	1	–	1	A
A. macrorhynchus	66	–	2	–	–	–	–	0	2	1	–	1	A
A. maderensis	66.8	–	2	–	–	–	–	0	2	1	–	1	A
A. manis	75.8	–	–	–	–	–	–	1	2	1	–	1	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
A. parvipinnis	52.1	-	2	-	-	-	-	0	2	1	-	1	A
A. platyrhynchus	64	-	2	-	-	-	-	0	2	1	-	1	A
A. riveri	40.5	-	2	-	-	-	-	0	2	1	-	1	A
A. saldanha	81	-	-	-	-	-	-	1	2	1	-	2	A
A. spongiceps	50	-	-	-	-	-	-	0	2	1	-	3	A
Genus ASYMBOLUS													
A. analis	57	-	-	-	-	-	-	0	3	1	-	2	A
A. vincenti	48	-	2	-	-	-	-	0	3	1	-	2	A
Genus ATELOMYCTERUS													
A. macleayi	51	-	-	10	-	-	-	0	1	1	-	2	A
A. marmoratus	53	-	2	-	-	-	-	0	1	1	-	1	A
Genus AULOHALAELURUS													
A. labiosus	67	67	-	-	-	-	-	1	1	1	-	2	A
Genus CEPHALOSCYLLIUM													
C. isabellum	86	-	-	-	-	-	-	0	2	1	2	3	A
C. sufflans	95.5	76.5	2	21	-	-	-	0	2	1	2	2	A
C. ventriosum	100	-	-	14.5	10	-	-	0	3	1	2	3	A
Genus CEPHALURUS													
C. cephalus	24	19	2	10	-	-	-	0	2	1	-	1	A
Genus GALEUS													
G. arae	43	-	-	-	-	-	-	1	2	1	2	1	A
G. eastmani	50	36.5	2	-	-	-	-	0	2	1	-	1	A
G. melastomus	90	42	-	-	-	-	-	0	2	1	2	1	A
G. nipponensis	66	54	-	-	-	-	-	0	2	1	-	1	A
G. piperatus	28	-	-	-	-	-	-	0	2	1	-	1	A
G. polli	41.5	-	-	7	-	-	-	1	2	1	-	3	A
G. sauteri	43.5	-	-	12	-	-	-	0	3	1	-	1	A
Genus HALAELURUS													
H. boesemani	45	-	8	7	-	-	-	0	2	1	-	3	A
H. buergeri	49	40.5	-	-	-	-	-	0	2	1	-	1	A
H. canescens	62.5	-	2	-	-	-	-	0	2	1	2	2	A
H. hispidus	25.5	-	-	-	-	-	-	1	2	1	2	1	A
H. immaculatus	75.5	-	-	-	-	-	-	1	2	1	-	1	A
H. lineatus	49	-	16	-	-	-	-	0	2	1	2	2	A
H. lutarius	35	-	22	10	-	-	-	1	2	1	2	3	A
H. natalensis	47	47	22	-	-	-	-	0	3	1	2	2	A
H. quagga	35.0	-	-	8	-	-	-	0	3	1	-	1	A

Appendix I (Cont'd.).

Taxon	Length (cm)	Length at maturity (cm)	Fecundity	Birth length (cm)	Gestation (mo.)	Age at maturity (yrs)	Life span (yrs)	Mode of reproduction	Zone	Habitat	Diet	Latitude	Source
Genus HAPLOBLEPHARUS													
H. edwardsii	60	41	2	10	–	–	–	0	3	1	2	2	A
H. fuscus	66.5	59.5	–	–	–	–	–	0	1	1	2	2	A
H. pictus	53	–	2	11	4	–	–	0	1	1	–	2	A
Genus HOLOHALAELURUS													
H. punctatus	25	21	2	–	–	–	–	0	2	1	2	2	A
H. regani	41	36.5	2	13	–	–	–	0	2	1	2	3	A
Genus PARMATURUS													
P. pilosus	64	–	–	–	–	–	–	1	2	1	–	1	A
P. xaniurus	51	–	–	–	–	–	–	0	2	1	2	1	A
Genus PORODERMA													
P. africanum	93	68.5	2	14.5	6	–	–	0	1	1	2	1	A
P. pantherinum	73	59.5	–	–	–	–	–	0	1	1	2	1	A
Genus SCHROEDERICHTHYS													
S. bivius	70	40	2	–	–	–	–	0	3	1	–	2	A,14
S. maculatus	34	–	2	–	–	–	–	0	2	1	2	1	A
S. tenuis	70	–	–	–	–	–	–	1	2	1	2	1	A
Genus SCYLIORHINUS													
S. canicula	60	44	2	9.5	11	–	–	0	2	1	2	1	A
S. capensis	85	69	2	30	–	–	–	0	3	1	2	2	A
S. cervigoni	76	–	–	–	–	–	–	0	2	1	–	3	A
S. haeckellii	40	–	–	11.5	–	–	–	0	2	1	–	3	A
S. hesperius	47	–	–	–	–	–	–	1	2	1	–	1	A
S. retifir	41	–	–	10	9	–	–	0	2	1	–	1	A
S. stellaris	125	–	2	16	–	–	–	0	3	1	2	1	A
S. torazame	39	–	–	8	–	–	–	0	3	1	–	1	A
S. torrei	26	–	–	–	–	–	–	1	2	1	–	1	A

Source references: (A) Compagno, 1984; (1) Casey et al., 1985; (2) Radtke and Cailliet, 1984; (3) Branstetter et al., 1987; (4) Tucker, 1985; (5) Beamish and McFarlane, 1985; (6) Bowman and Eppi, 1984; (7) Nammack et al., 1985; (8) Natanson and Cailliet, 1986; (9) Cailliet et al., 1985; (10) Natanson et al., 1984; (11) Welden et al., 1987; (12) Branstetter and McEachran, 1986; (13) Ebert, 1986; (14) Manni, 1986.

Appendix II

A breakdown of the data into sets associated with a particular analysis.

Analysis	No. orders	No. families	No. genera	No. species
1. Impact of length	4	16	-	228
2. Classwide correlation	4	16	-	228
3. Taxonomic level				
Order and family	4	16	-	228
Family and genus	-	6	28	159
4. Mode of reproduction				247
5. Covariation				
- family effects	-	10		81
- genus effects	-	9	14	65
- mode of reproduction effects	-	10		81
- ecological effects	-	10		81
6. Life history variation Analysis of ecology	-	11	-	223